

STUDIES IN THE UREDINALES WITH
PARTICULAR REFERENCE TO CEREAL RUSTS

A dissertation submitted to the
University of Edinburgh for the degree of
Doctor of Philosophy

by

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May, 1950

ACKNOWLEDGEMENTS

The writer wishes to express his thanks to:-
the Edinburgh and East of Scotland College authorities
and particularly to Mr R. G. Heddle for so willingly
supplying facilities and equipment necessary for the
study here written up; the Air Ministry Meteorological
Office, Edinburgh, for allowing the writer to copy the
necessary weather records; the two farmers near
Melrose for providing land and facilities for
experiments; those people who so willingly gave the
writer information on barberry localities, and on
many other matters connected with the study.

Lastly but by no means least the writer wishes
to record his appreciation of the stimulating
interest shown by Dr Malcolm Wilson of the Royal
Botanic Gardens, Edinburgh under whom the work was
carried out.

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SECTION 1.

PUCCINIA GRAMINIS.

PART I

INTRODUCTION

1. General background

Since very early times the cereals have been among the most important food producing plants of the human race. The rusts which attack these cereals are their most serious diseases. It is therefore of little wonder that considerable time and energy has been expended on these rusts by many hundreds of personnel during about the last half century. Of great importance as any is the rust known as black or stem rust Puccinia graminis.

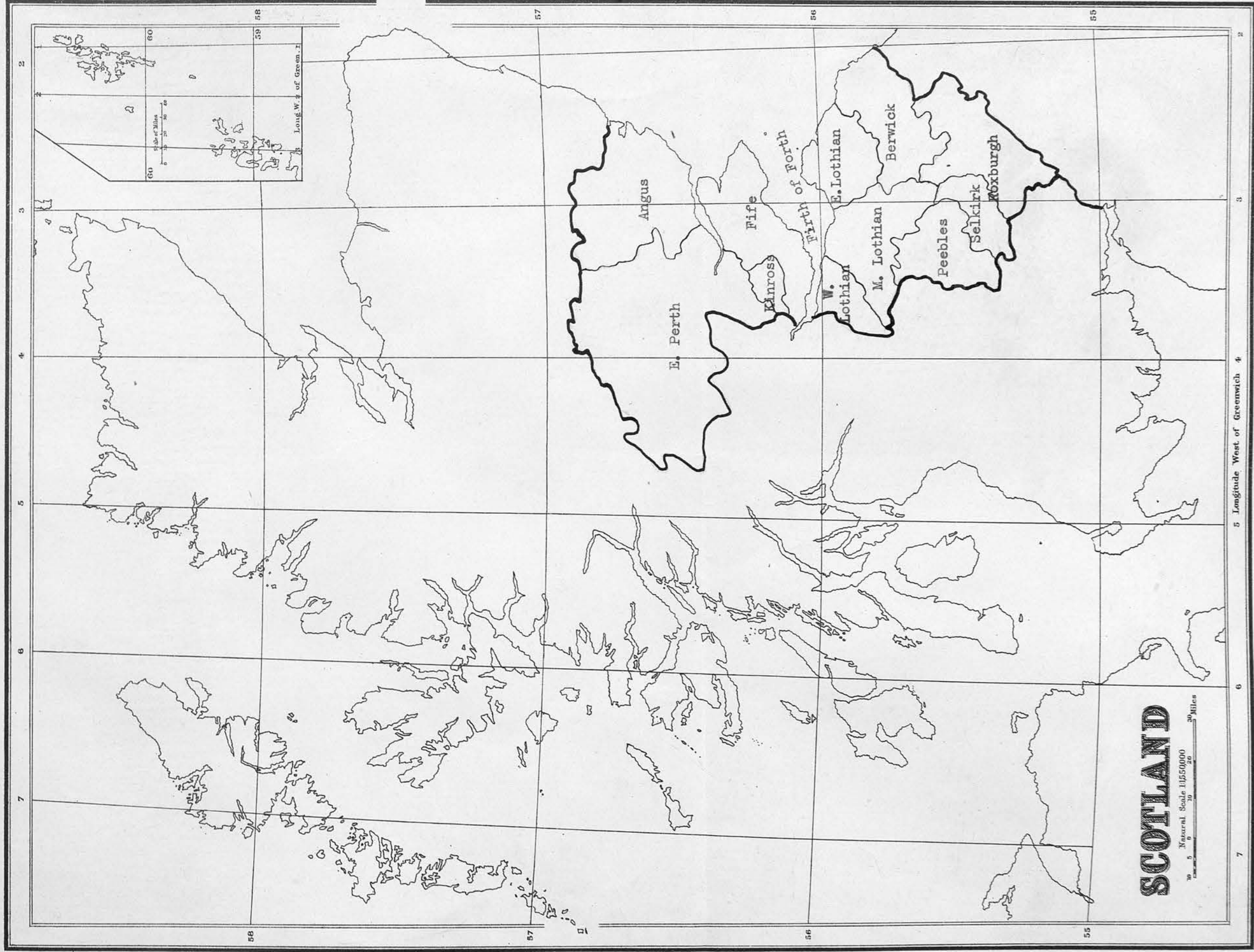
The severe losses brought about by this disease have been indicated in scores of publications, scientific and popular. A large proportion of the work on cereal rusts generally and black rust in particular has been carried out in Canada and the United States. As far as Britain is concerned very little work on disease has been published. Probably the most comprehensive paper was that of Mehta (1923) working at Cambridge. A paper three years later (Maxwell & Wallace 1926) gave a brief account of some work in Scotland. Of a rather more general nature are papers by Broadbent (1921), Dillon Weston (1929), Biffen (1931), and Jenkin and Sampson (1921).

In the late summer of 1945 many reports were received of severe attacks of black rust on cereals, and in particular on oat crops in the Border counties. It soon became apparent that the rust could assume serious proportions. It was therefore decided to

I investigate the disease as it occurs in S.E.Scotland. This is the area covered, as far as advisory work is concerned, by the Edinburgh and East of Scotland College of Agriculture, which includes counties of Perth (East), Kinross, Angus, Fife, Lothians, Peebles, Selkirk, Roxburgh and Berwick. The counties in which this study on cereal rusts was carried out are shown in Fig.1.

Fig. 1.

Map showing counties in which the incidence of Cereal Rusts was investigated.



PART II

THE DISEASE IN THE EARLY NINETEENTH CENTURY

Before proceeding to give an account of the problem at the present time it is well worth while considering extracts from an extremely interesting book written in 1809 (Sinclair 1809) which contains several sections dealing specifically with black rust in the Border counties.

In his introduction Sir John Sinclair the first President of the Board of Agriculture writes 'Having received from various quarters towards the end of August and beginning of September last the distressing intelligence that in some of the southern counties of Scotland the crops of wheat had suffered in a most alarming degree from the blight, the Rust and the Mildew I resolved to circulate some heads of enquiry for the purpose of procuring all the information I could upon the subject.' As was usual at the time the terms 'blight,' 'rust,' and 'mildew' are used very loosely throughout the book. It is, however, worth quoting certain sections which indicate that black rust was sometimes severe in southern Scotland even in those days.

The book is in two parts. The first is a general account of the disease by Sinclair, which is based on the letters he received in reply to his enquiries. This second half of the book consists of a selection of these letters.

The only mention of barberry comes in the general account - 'the influence which the barberry

bush is said to possess of producing a most noxious effect upon corn and particularly upon wheat and oats' - Sinclair does not commit himself in giving an opinion on whether or not the barberry is harmful.

Sir Joseph Banks is reported as suggesting that the mildew - 'might be prevented or at least rendered less extensively injurious if farmers were by way of precaution to search diligently in the spring for young plants of wheat infected with the disease and carefully to extirpate them as well as all diseased grasses, for several of them are subject to this or a similar malady. Diseased plants and grasses have the appearance of orange colour or of black stripes in their straw or on their leaves.'

Some interesting extracts taken from a few of the letters contained in the second part of the book follow:-

N. of England, Chillingham:

- 'the cause of the injury from the rust owing, one to the hot sultry weather, and the other to the wet, close, cloudy weather, in the latter end of July and beginning of August.'

Robert Kerr, Esq., Covey House, Nr Ayton, Berwickshire:

'The mildew began to make its appearance about the 4th to the 8th of July and which was followed for several weeks by much misty and rainy weather attended by considerable heat and little wind. The disease upon the wheat straw, here named mildew, and which has done so much injury this season in Berwickshire, Teviotdale, and the northern part of Northumberland consists of a species of lichen of an

oblong pointed form like a boat or wherry or canoe having white edges, and a black pulverated disc, each individual spot being about an eighth of an inch long and about a sixteenth in breadthIt progressed .. until in many instances whole fields put on an universal blackened appearance, and the grains in the ear were found to be more or less false or deaf or unimpregnated. the wheat crop was very much lodged by heavy rains about the beginning of August .. the straw became utterly unfit for fodder.

Some years ago (I think six or seven) many fields of oats were exceedingly injured a little before harvest The small pedicels of the florets, or the ramifications of the heads became attacked by a fine black powder, which however was not microscopically examined, though perhaps it might likewise have been found to be a species of parasitical lichen. In consequence of this affection a considerable loss of grain was sustained, perhaps equal to from six to eighteen bushels an acre.'

Dr Douglas of Kelso:

'..... where the wheat suffered most it (the straw) was loaded with a blackish coloured rough fungus The ear was but partly filled with a small shrivelled grain and in many instances was quite empty the colour of the wheat began to change to a gradually deepening brown and it was remarked that the darker the colour, the worse was the crop.'

The disease was also troublesome to the north of the Forth as the following extracts show:-

Fife:

'... the under part of the stalk (wheat) was often sound, while the upper was black and crusted; the straw not of any use.'

Forfarshire: 'Communication from a respectable Gentleman Farmer.'

'This year (1808) my shoes were red with walking a very short distance through it (the wheat) ... I saw the rust perfectly distinct upon some stalks of unripe oats, but I cannot say whether it would have injured the grain or not.'

These extracts obviously refer to black rust. In many cases the teleutospore stage only being mentioned and one instance is admirably described. The observations on the prevailing weather conditions are interesting particularly in the light of modern research.

on of the common barberry. The 'blight' or 'mildew' connected with the plant is mentioned in many of them. The remarks on the bush and disease from two classic Flores are given below:-

Kewille, S.K. Flora Edinensis, 1834.

Barberis vulgaris

Hab. Hedges, road side near Queensferry.

Occasionally about Edinburgh.

Puccinia graminis

It is most injurious to corn and in an agricultural point of view of some importance; but a remedy against its attacks has not yet been discovered and probably never will.

PART III

THE OCCURRENCE AND DISTRIBUTION OF THE
COMMON BARBERRY

1. HISTORICAL NOTE:

A little over eighty years ago, Anton de Bary connected the Aecidium berberidis of Persoon with his (de Bary's) Puccinia graminis. For centuries previously, however, agriculturalists and others had observed that somehow the rust (or mildew as it was often called) of wheat was usually most severe when the common barberry, Berberis vulgaris, was growing near the crop.

2. MENTION OF THE BARBERRY IN FLORAS:

Most of the floras of south Scotland, old and more recent, contain notes on the occurrence and distribution of the common barberry. The 'blight' or 'mildew' connected with the plant is mentioned in many of them. The remarks on the bush and disease from two classic floras are given below:-

Greville, R.K. Flora Edinensis, 1824.

Berberis vulgaris

Hab. Hedges, road side near Queensferry.

Occasionally about Edinburgh.

Puccinia graminis

It is most injurious to corn and in an agricultural point of view of some importance; but a remedy against its attacks has not yet been discovered and probably never will.

Aecidium berberidis

Hab. Not uncommon, Carlowrie.

It is still a popular belief that barberry bushes produce the blight in wheat; accidental circumstances may have tended to confirm this opinion, but the two plants are entirely different.'

Johnston, Flora of Berwick, 1829:

Berberis vulgaris

'Hab. Hedges occasionally.

The leaves are in general more or less covered with a small orange coloured fungus whence seems to have originated an opinion entertained by many practical farmers that the barberry is injurious to corn by infecting it with a mildew. To determine the accuracy of this statement, it should first be proved that the mildew of the barberry and of corn is owing to the same species of fungus!

The Field Club Flora of the Lothians gives as localities for the common barberry 'Hedges. Dunbar, Tynninghame, Humble, Longniddry, Crichtoun, Colinton, Currie, Dalmeny, South Queensferry.'

Some localities are also given in Young's Flora of Fife and Kinross, and Balfour's History of Peeblesshire.

3. PRESENT DAY DISTRIBUTION:

Since the present study was commenced in 1945 every opportunity has been taken of noting the occurrence of the common barberry in S.E. Scotland.

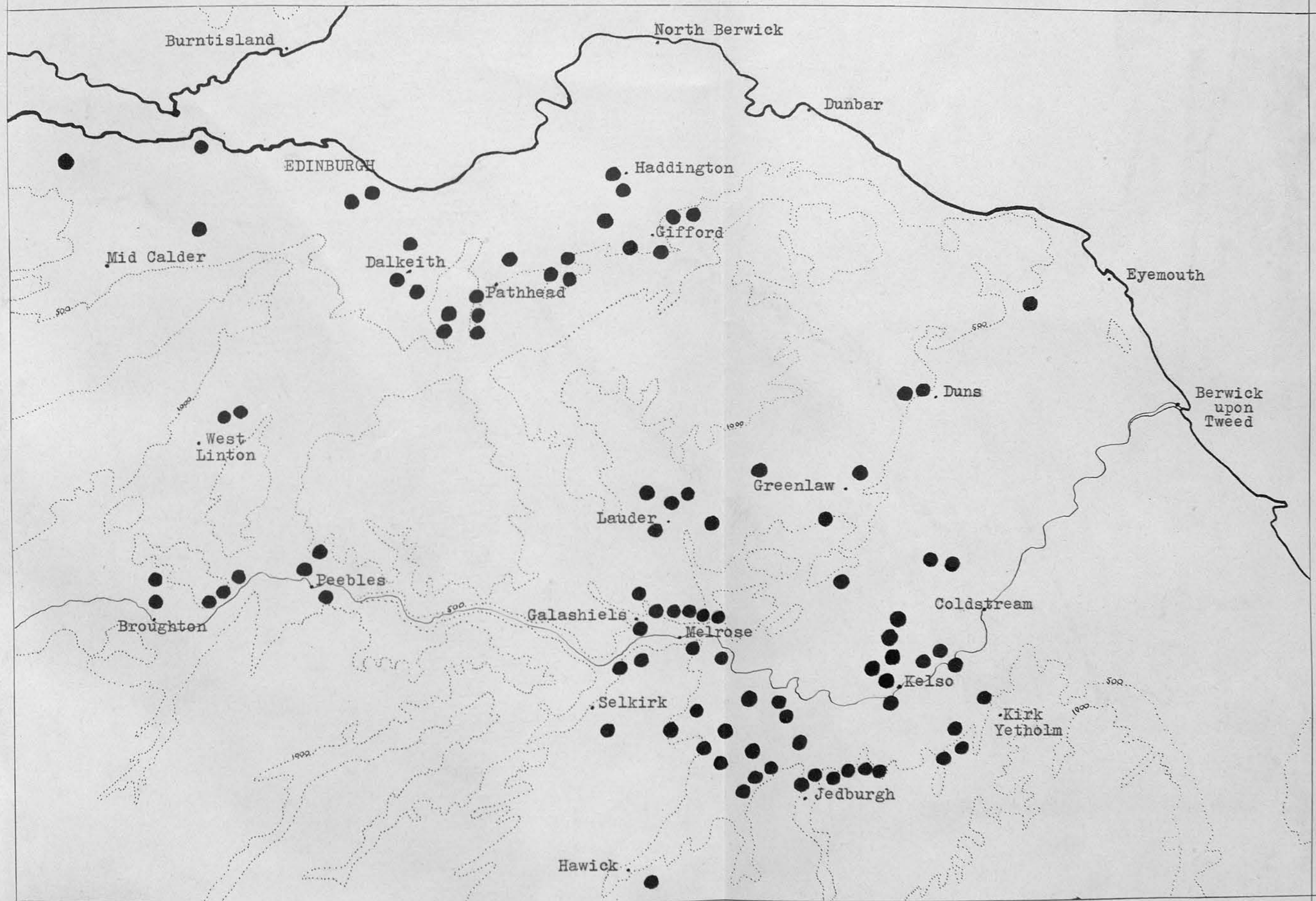
Several bushes were brought to the attention of the writer by the mycologists in Edinburgh as well as by several of the East of Scotland College staff. It should be made clear from the start that by a barberry 'bush' the writer means one barberry locality. A 'bush' may be anything from a few branches to a solid hedge about 400 yards long. The main thing is that wherever barberry leaves are present, they are a possible source of black rust. Obviously a long solid hedge will provide more inoculum in the spring than a solitary bush (a bush as usually understood), but even so the latter could under suitable weather conditions be responsible for providing inoculum for a very wide area.

By far the greatest proportion of the barberry bushes now located were found by the writer. Wherever a trip was made out of Edinburgh a look out was kept for the barberry and in the course of about four years a considerable number of bushes have been located.

Figs.2 and 3 show the known distribution of the common barberry. Fig.3 contains the area north of the Forth. From Fig.2 it will be seen that the barberries are particularly numerous in Roxburghshire. The hedges around and about Kelso, Melrose and Jedburgh are particularly well supplied. The bushes are rather more scattered in the other counties in this area. It is rather interesting to observe that in mid and East Lothian the bushes are almost entirely confined to the 500 foot contour line. This feature can also be seen in the Border counties but in these there are many bushes on the lower land as

Fig. 2.

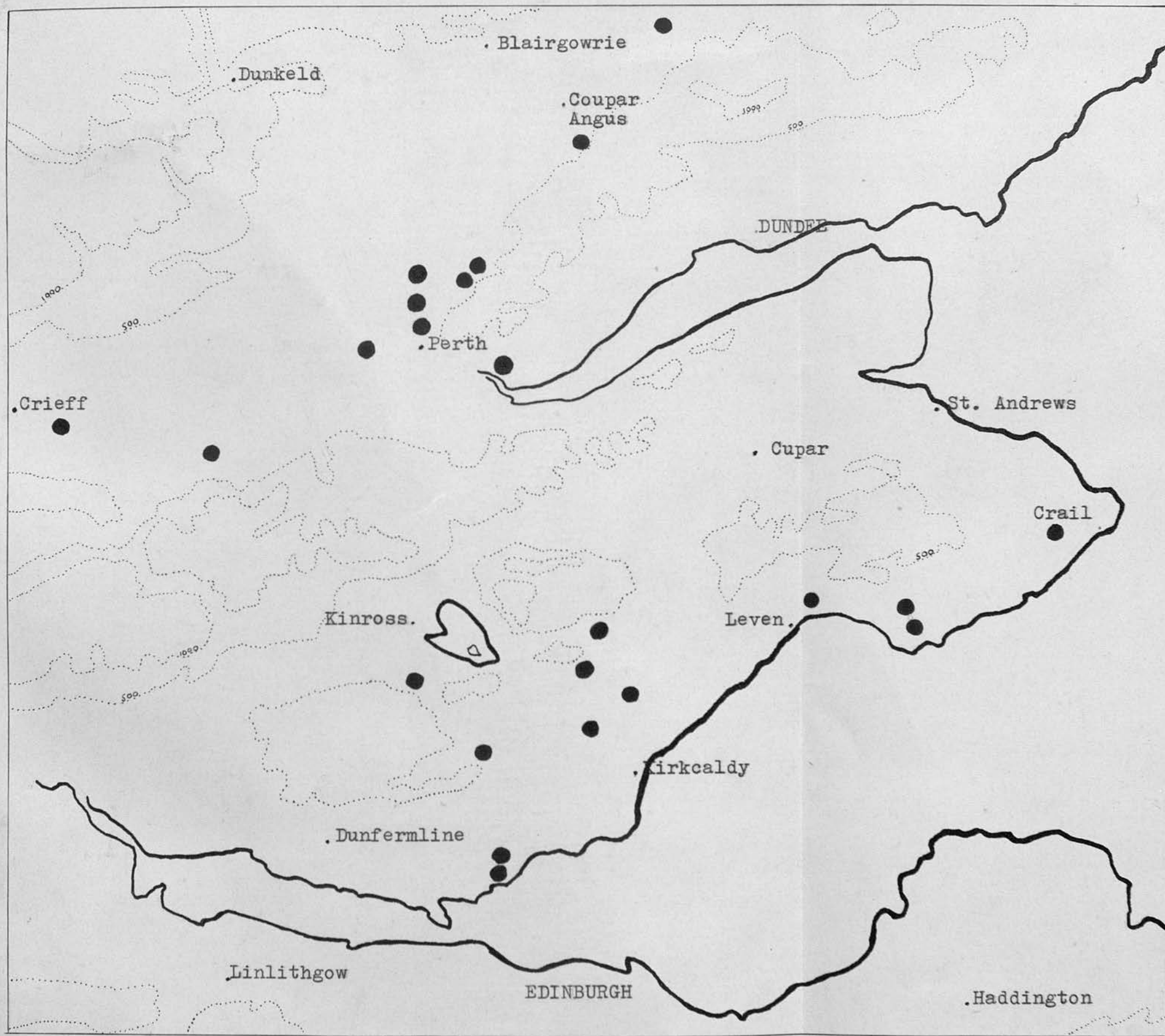
DISTRIBUTION OF BERBERIS VULGARIS IN AREA SOUTH OF THE FORTH.



● *Berberis vulgaris* locality

Fig. 3.

DISTRIBUTION OF BERBERIS VULGARIS IN AREA NORTH OF THE FORTH.



● *Berberis vulgaris* locality

well. The frequency of the barberry bushes in the Tweed valley has been noted by Dennis (1944).

In this area south of the Forth, if one excludes land over 1,000 feet, it can be said that there is no field further than seven miles from a barberry.

To the north of the Forth the barberry is much less frequent. There are scattered bushes around the southern coastal strip of Fife and a few about the town of Perth. Otherwise the plant is rather rare.

Maxwell and Wallace (1926) state that the common barberry is probably not so common as it once was, but is found widely distributed in a healthy condition over the southern half of Scotland. It is of course impossible now to judge the accuracy of this statement. Those writers may have looked at the barberries at the wrong time, but at the present day very few of the barberries known fail to develop aecidia each season. Two lots of bushes which have not been seen bearing aecidia are those located near South Queensferry. It is difficult to explain their healthy condition, but the nearness of the sea may have something to do with it. They are nearer the sea than any of the bushes along the Fife coastal strip, all of which are regularly infected.

It is well known that certain cultivated species of *Berberis* are susceptible to the black rust fungus. In the area under review, however, no cultivated species has been found to be infected.

4. MAHONIA AS ALTERNATE HOST

In the very early spring of 1949 considerable teleutospore infection was observed on couch grass in

an area away from barberries. At least it was known that the rust had not spread sufficiently far from barberries in 1948 to infect this grass. However, Mahonia aquifolium was growing in some quantity near this infected couch grass. In mid June aecidia began to appear on the berries of the mahonia and by 12 July the adjacent couch stems were bearing uredosori. Berries bearing aecidia were then taken back to the greenhouse, and the aecidiospores were inoculated onto barley seedlings. Within ten days uredosori were present on the inoculated leaves. The mahonia berries can then also function as an alternate host to Puccinia graminis and in an area where barberry was known to be scarce, mahonia could perpetuate the disease.

5. THE FORM OF THE INFECTION ON THE BARBERRY:

Details of the date of appearance of the spore forms of the rust are given in a later section, but while dealing with the barberry a few remarks on the general form of the infection may be given.

Infection usually becomes quite severe although it varies somewhat from season to season. The main infection occurs on the leaves, only the young leaves becoming infected. A leaf showing typical infection is given in Fig.4. The berries are also frequently infected as shown in Fig.5. An enlarged single berry is shown in Fig.6. The aecidia on the berries never take on the typical pitted formation, but are instead like little tubular horns. Further remarks on these tubular horns are given in a later section.

From July onward, the barberry produces new



Fig.4.

Typical aecidial
infection on
barberry leaf.

Fig.5.

Portion of barberry
stem showing infection
on berries.



Fig.6.

Berry enlarged showing
aecidia.



growth. The young stems are often quite severely infected and distorted. Aecidia develop also at the junction of the stem and thorns and the resulting swelling completely merges these organs at this point.

PART IV

THE HOST RANGE

1. PREVIOUS RECORDS IN BRITAIN

(i) Scotland:

Maxwell and Wallace (1920) record black rust on the following hosts in south Scotland:-

Triticum vulgare, Hordeum vulgare, Avena sativa and Secale cereale, and the grasses Agropyrum repens, Agrostis vulgaris, Bromus sterilis and Dactylis glomerata. Dennis and Foister (1942) referring largely to another list (Wilson, 1934) include also the following grasses as hosts:-
Aira caespitosa, Alopecurus pratensis,
Arrhenatherum avenaceum, Briza media, Festuca pratensis and Lolium spp..

(ii) England:

The rust has been observed on several grasses in Yorkshire (Bramley 1948) and the host list given is Agropyrum repens, A.caninum,
Agrostis spp., Arrhenatherum elatius, Avena fatua,
A.sativa, Dactylis glomerata, Hordeum distichum,
Lolium perenne, Secale cereale, Triticum vulgare.

2. HOSTS IN S.E.SCOTLAND

In S.E.Scotland the writer has found the rust on the four cereals and on fourteen genera of the grasses. These hosts are set out in alphabetical order below (cereals first) together with a few notes on the distribution and occurrence of each.

(i) Cereals found infected:

Avena sativa Linn.. (oats).

This is the cereal which is most

commonly and frequently found infected. In Roxburghshire particularly the attack is in certain seasons severe. In the Lothians and counties north of the Forth, oats are very rarely infected.

Hordeum vulgare Linn.. (barley)

Growing near barberry bushes barley is occasionally found bearing sori of black rust, but the amount of infection is always slight.

Secale cereale Linn.. (rye)

Crops of rye are found scattered over the area, but infection is rarely seen. The only place where the crop is occasionally found to be attacked is in the Ladybank area of Fife where probably more crops of rye are grown than in any other part of S.E.Scotland.

Triticum vulgare Host.

Infection of wheat is rare in S.E.Scotland. It has only been seen a few times and mainly in the Border counties. However one field in west Berwickshire was found to be severely infected in August 1947.

Thus normally black rust is not an important disease of wheat, barley or rye. The disease is, however, serious on oats in certain seasons, but then only in the Border counties. Some further

discussion on black rust of oats follows later (page 42).

(ii) Grasses found infected:

Agropyrum repens Beauv.. (Couch grass)

If a barberry bush is infected with

Puccinia graminis then any couch

grass growing near will always be

found bearing uredosori or

teleutosori according to the time

of year. No exception to this has

ever been observed. This grass is

therefore by far the one most

commonly infected. The first

uredosori develop on the upper leaf

sheaths just below the auricles of

the leaf blades. When growing near

the barberry the infection on couch

grass generally becomes very severe

on all parts of the plant,

inflorescence included.

This grass is usually the

first to become infected in each

season.

Agrostis canina Linn.. and A. vulgaris With..

(Bent grasses)

Bent grasses are frequently found

bearing infection but not so

commonly as the previous grass.

The leaf blades usually become

infected later in the season.

Leaf blade infection is rare with

other grasses.

Alopecurus pratensis Linn.. (Meadow Foxtail)

Infection has only been observed about half a dozen times, mainly in Roxburghshire. It does not become infected until rather late in the season and then rarely severely.

Anthoxanthum odoratum Linn.. (Sweet vernal grass)

Black rust infection is extremely rare on this grass. It has been seen three times only. Once each in mid Lothian, Peeblesshire, and Roxburghshire. The latter locality yielded the greatest amount of material. Infected plants were in each case growing in boggy ground and were rather green for the time of year (October 1949). Uredosori and teleutosori were usually seen to be present near ground level. One flowering stem was found with sori near the inflorescence.

As is well known, sweet vernal grass is usually the first grass to flower. Thus green stems are unusual late in the season. It is thought that perhaps one reason why this grass is so rarely found to be infected is because it is usually in a rather senescent condition when uredospores are present and spreading.

Arrhenatherum avenaceum Beauv.. (Tall or False

oat grass)

This grass is frequently infected particularly in the Border counties.

Infection appears some weeks later than it does on couch grass.

Avena fatua Linn.. (Wild oat)

The wild oat is not at all common in Scotland, but is occasionally found near barberry bushes and then may be infected.

Bromus asper Murr.. (Wood Brome Grass)

This grass is rarely seen in the neighbourhood of barberries. However near Humbie (E. Lothian) the grass grows near a rather large barberry and it becomes infected each season, but always rather slightly.

Bromus sterilis Linn.. (Barren Brome grass)

Infection has been observed on this species in several localities in the Lothians. It is rather an early developing grass and the amount of infection present is rarely very great.

Cynosurus cristatus Linn.. (Crested dog's tail)

Only in a few localities in the Borders is this grass known to be infected. Infection seems to occur fairly late in the season, and as was the case with sweet vernal, sori are

present only on the internodes near the ground level. Only a few of the plants in any one locality are infected.

Dactylis glomerata Linn.. (Cock's foot)

In the Border counties the flowering stems of this grass frequently bear sori. Uredosori are rarely present for more than a very short time. The fungus forms teleutosori very soon after infection.

Festuca rubra Linn.. (Red fescue)

Although looked for previously, infection on this grass was not found until July 1949. Only in a few scattered localities is infection known, and it is always rather slight.

Hordeum murinum Linn.. (Wall barley-grass)

H. murinum is not often found growing in the vicinity of barberry. However in a few centres in mid Lothian it is found and then becomes infected.

Phleum pratense Linn.. (Timothy)

Much has been written on the possible relationship between this grass and Puccinia graminis. A careful search has been made wherever this grass grows near a source of infection. However, only once, in November 1946, was it found bearing teleutosori on

a few flowering stems. These stems were collected, kept outside over winter and the following spring inoculated onto young barberry leaves in the greenhouse. Quite good infection of the barberry resulted.

The stem rust on timothy is often referred to as Puccinia phlei-pratensis Erikss. et Henn., although it is indistinguishable from P. graminis except that it is said not to infect barberry. It is unfortunate that infected plants were not found again, but in this one instance infection of the barberry did occur.

Poa pratensis Linn., and P. trivialis Linn..

(meadow grasses).

In July 1948 teleutosori were found on Poa trivialis in two centres in Roxburghshire. As far as is known, this is the first record of Puccinia graminis on Poa in this country. Since then the grass has been found to be infected in several other localities. Poa pratensis is also occasionally affected. The infection is often severe. Fig.7 shows the typically infected flowering stem and inflorescence. The sori on the latter may be seen more clearly by using a lens.

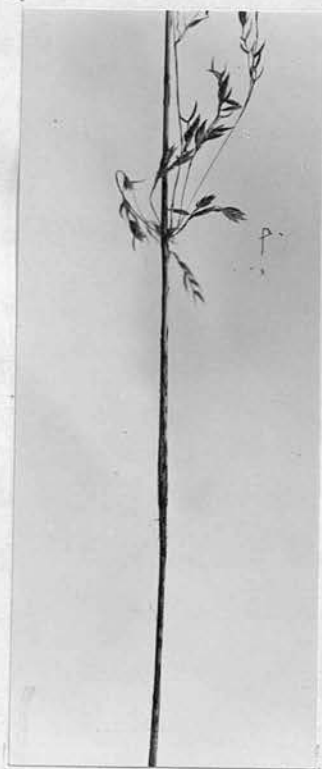


Fig. 7.

Teleutosori on Poa pratensis.

Trisetum flavescens Beauv.. (Golden oat grass)

Like Bromus asper this grass is not often found growing near barberry bushes. There are, however, some plants in the Melrose area growing beneath bushes and they are usually infected.

A few of the other common grass genera e.g. Aira, Brachypodium, Holcus, and Lolium are frequently found growing near infected barberries, but no infection has been seen on them. The grass Briza media is of interest because according to a Scottish record (Dennis & Foister 1942) uredosori of black rust have been found on it growing in a remote corner of Perthshire. Unfortunately, it has not been possible to visit the area and so no comment can be made. The grass has not been found by the writer anywhere near a source of infection.

By the month of August black rust was fairly widespread and often severe particularly on oat crops in the Border counties. Upon investigating reports of crops attacked it became apparent that the worst attacked were adjacent to or within a few hundred yards of barberry bushes.

Acrida were still present on 11 September. They were last seen on 16 October in Fife. Infection did not spread far from the barberries in this season.

PART V

THE SEASONAL DEVELOPMENT OF THE DISEASE

1. THE DEVELOPMENT OF THE DISEASE EACH SEASON

The life cycle of Puccinia graminis is one of the most complex and yet most interesting in probably the whole plant kingdom. It is unnecessary here to go into the history of our knowledge of the fungus. Suffice it to say that it was only in the last quarter century that all the spore stages were linked up correctly.

The various spore forms follow each other in strict regularity, but the actual time of appearance of the forms varies from season to season, depending very largely upon the prevailing weather conditions.

Detailed observations on the fungus were not made until September 1946, but it is possible to give a few general remarks for 1945. The general progress of the disease in S.E. Scotland from 1945 until 1949 is then as follows:-

1945: By the month of August black rust was fairly widespread and often severe particularly on oat crops in the Border counties. Upon investigating reports of crops attacked it becomes apparent that the worst attacked were adjacent to or within a few hundred yards of barberry bushes.

1946: Aecidia were still present on 11 September. They were last seen on 16 October in Fife. Infection did not spread far from the barberries in this season.

1947: On 3 April the barberry buds began to show green tips in mid Lothian, and the first spermatia appeared on these bushes on 15 May. By the end of May aecidiospores were being liberated. Aecidia were present only until the end of August, which was rather in marked contrast to the previous year. In 1947 the teleutospores germinated later than usual (compare the date of appearance of aecidia in 1948 and 1949) but apparently they then all germinated in a comparatively short time i.e. had finished germination by about mid August.

The first uredosori were found on couch grass on 16 June. The disease developed rapidly and spread and by the middle of July oat crops were infected in the Border counties. By harvest time, many such oat crops presented a completely blackened appearance.

Uredosori were present on odd green plants such as volunteer oats in root fields until about the end of November. No uredospores were found later than this.

In 1947 teleutospores appeared rather early on all hosts. By the end of July uredospores were scarce on couch grass.

By the autumn, infection was severe on many grasses and cereal crops (particularly on oats) even several miles from known barberry bushes. Conditions were then apparently ideal for the development and spread of the disease

throughout the season. seen after August.

1948: On 19 March the barberry buds were just showing red tips and by 12 April were rapidly unfolding. The first spermatia were seen four days later. Aecidial beginnings were present on 8 May and were liberating spores about a week later. were present on buds in

Aecidia were observed until the end of September. late June. The amount which

The first uredosori were found on 11 June. These sori were about a week later in appearing after the aecidial beginnings were observed than in 1947, i.e. in 1947 about three weeks elapsed between aecidiospore and uredospore appearances, in 1948 four to five weeks elapsed. Uredospores were present until mid November. rose and couch and cereals growing on

Teleutosori were not present in any quantity until mid August. in 1948 were then

In 1948 infection did not spread far from the barberries. late in the season.

1949: Judging by the appearance of spermatia the teleutospores germinated very sporadically in the spring of this year. A few spermatia were seen in one locality in Fife on 25 April, but even a fortnight later, spermatia were still absent in many other localities. General infection did not appear until 1 June, but then many bushes became severely infected. In some cases the subsequently developed aecidia covered almost the entire leaf surfaces.

Aecidiospores were not seen after August.

As would be expected the uredo soral appearance was just as sporadic. The first

were seen on 14 June but they did not become general until the end of the month.

Teleutosori made their appearance rather early in 1949. Some were present on oats in

mid July (in an area where uredosori did not appear until late June). The drought which

existed throughout almost the entire season

undoubtedly made conditions unfavourable for uredospore development. On some infected

grasses, particularly those growing on shallow soil, very few uredospores were produced.

During October scattered infection was

observed on such plants as volunteer cereals

in root crops and couch and cereals growing on

middens, often a mile or so away from known

barberries. The conditions in 1949 were then

apparently favourable for the spread of the

disease, but only late in the season.

Therefore reviewing the years 1945 to

1949 inclusive it may be said that black rust

was widespread and severe in 1945 and rather

worse even in 1947. In 1946 and 1948 the

disease was confined only to the vegetation

near the barberries. 1949 was rather an

intermediate year. In this latter year the

disease did spread away from the barberries,

but too late in the season to affect the

cereal crops.

2. THE TIME OF APPEARANCE OF TELEUTOSPORES

If one compares the approximate time of appearance of teleutospores particularly on oats in the three seasons for which detailed records are available, viz. 1947-9, it will be observed that they appeared earlier in 1947 and 1949 than in 1948. In the summer of this latter year the average temperature was lower and the average relative humidity was higher than in the summers of the other two years (for details see section of meteorological conditions and rust incidence). This observation fits in with the findings of Gordon (1933) who showed that all the physiologic forms of P. graminis avenae developed teleutospores more rapidly at relatively high temperatures than at lower temperatures. He also showed that teleutospore development on mature plants (as opposed to seedlings) was rather increased by a low relative humidity.

3. OVERWINTERING OF THE RUST

As indicated in a previous section, there are sufficient and more barberries in the south east of Scotland to account for all the black rust which appears each season. However, the question arises out of the possibility of overwintering of the rust by some means or other so that if all the barberries (and Mahonia) were removed, the disease could re-appear each season.

(i) Uredospore stage

The obvious suggestion is that the rust may survive in the uredospore stage. This possibility has been considered since the commencement of the

work. A search has been made each winter for uredosori. They are very seldom found after November. In 1947 a few uredosori were, however, found on 9 December. They were present on oats growing near a midden which were still somewhat succulent and green. The uredospores were tested for germination on 1% agar but not one germinated. This is the latest date that uredospores have been seen under natural conditions.

As already indicated black rust was widespread in the autumn of 1947. The winter following was very mild and special notice was taken in the late spring and summer of 1948 to see if fresh infection appeared for example, on couch and other perennial grasses which were infected in 1947 and were growing well away from barberries. Uredospores were never seen to develop. Thus even in a mild winter black rust apparently does not survive in the uredospore stage.

(ii) Perennial Mycelium

It has been suggested that the rust may overwinter as internal mycelium in the grass hosts. The previous paragraph indicates that this does not happen. However, in order to investigate this point more fully, severely infected clumps of couch grass and bent grass were potted up in large pots in the late summer of 1947. The pots were then kept in an unheated greenhouse during the following winter and spring. Fresh uredosori of black rust did not reappear although both sets of plants were flourishing.

The writer is therefore in complete agreement with the statement made by Maxwell and Wallace (1926)

that 'there is no evidence that the disease is carried over the winter by means of uredospores, and the destruction of barberries will almost certainly result in the disappearance of the disease.'

(3) Germination

It is well known that under natural conditions the teliospores of black rust germinate in the spring. The writer has obtained good germination of the spores by scraping them off infected material, which has overwintered outside and putting the spores onto the surface of ordinary tap water in a watch glass. From about mid March onwards quite a high percentage of the spores will be found to have germinated after about 24 hours under laboratory conditions.

Johnson (1931) was able to shorten the period of dormancy of wheat black rust teliospores by first freezing them, then following with an alternate wetting and drying sequence. Teliospores formed naturally in September germinated abundantly by this treatment at the beginning of December.

This method was tried using Scottish material. At the beginning of November teliospores formed naturally on couch grass were placed in a refrigerator for six days, the surrounding temperature being 12°C . The material was then removed and alternately wetted and dried (wet days wet, dry days dry) until the following April. Some of the spores were tested for germination at intervals, but spores submitted to this treatment did not germinate any sooner than spores left under normal conditions.

PART VI

OBSERVATIONS ON SPORE GERMINATION AND
INOCUATIONS

1. TELEUTOSPORES

(i) Germination

It is well known that under natural conditions the teleutospores of black rust germinate in the spring. The writer has obtained good germination of the spores by scraping them off infected material, which has overwintered outside and dusting the spores onto the surface of ordinary tap water in a watch glass. From about mid March onwards quite a high percentage of the spores will be found to have germinated after about 24 hours under laboratory conditions.

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This method was tried out using Scottish material. At the beginning of November 1946 teleutospores formed naturally on couch grass were placed in a refrigerator for six days, the surrounding temperature being 12°C. The material was then removed and alternately wetted and dried (two days wet, two days dry) until the following April. Some of the spores were tested for germination at intervals, but spores submitted to this treatment did not germinate any sooner than spores left outside under normal conditions.

Lambert (1929) also failed to germinate teleutospores any sooner by this method.

Various workers have also tried chemical stimuli to break dormancy and so hasten germination. The method advocated by Thiel and Weiss (1920) has been tried with some success. Their method is briefly as follows. Infected stems are first exposed to chloroform vapour for about one minute. This of course is to partially sterilise the stems to prevent moulds appearing too quickly. The rusted stems are next immersed in 1% citric acid for varying periods of time. Thiel and Weiss then put the spores to germinate by placing the treated material in small vials lined with moist filter paper, which were then corked. The vials were refrigerated at about 42°F. They found that optimum germination of 15% was obtained after 15 minutes exposure to the acid. Germination began after $2\frac{1}{2}$ days. Material treated on 25 February and then put to germinate near barberry leaves gave pycnidial beginnings 7 March.

By using this method teleutospores from Scottish material were made to germinate about three weeks earlier than material untreated. The first germination of treated material was obtained on 17 April. Untreated material from outside germinated on 4 May (this work was carried out in the spring of 1947 when the teleutospores germinated later than usual). Thiel and Weiss also apparently advanced the time of germination of their material only by a matter of weeks. If they had succeeded in obtaining germination before February they undoubtedly would

have stated so.

(ii) Barberry inoculation

The writer has experienced no difficulty in infecting small barberry plants. The technique adopted is briefly as follows.

Sections of the barberry about a foot long with roots attached are dug up from the base of established bushes. They were dug each season just as the buds began to unfold, and potted up in 9 inch pots. This seemed to be the best time for getting the portions of barberry bush to establish. Once the leaves had expanded, the plants did not 'take' in the pots.

Such potted plants become established within about a week and could then be inoculated from the appropriate teleutospore material. For this purpose an 'incubation chamber' was made. A wooden box 4 feet long by $2\frac{1}{2}$ feet broad and $2\frac{1}{2}$ feet high was fitted with a removable wooden lid into which were fitted two panes of glass. The inside of the box and underside of the lid were covered with sacking which was kept thoroughly soaked throughout the period when inoculations were being carried out. Thus when the lid was fitted the atmosphere inside the box was at 100% relative humidity. This created ideal conditions for teleutospore germination and infection of barberry.

Several pots containing barberry with leaves only two or three days old were placed in the bottom of the chamber. The appropriate rusted material was then placed in the bottom of a glass cylinder, wide enough to cover one pot. The cylinder was then

inverted over the pot. In this way the teleutospore material was suspended over the barberry leaves. Each pot to be inoculated was left for about 48 hours in the chamber, and then removed and stood on the bench in the greenhouse. As each barberry was removed care was taken to remove all the inoculum, so that odd portions of rusted straw were not left in the bottom of the chamber.

Spermatia usually appeared after about nine days, and aecidiospores followed about ten days later.

(a) Unusual aecidial formation

A constant feature of all aecidia produced under these greenhouse conditions was that instead of the usual pits developed under natural conditions, long cylindrical columns were formed. The columns were each about 2 to 3 m.m. long and $1/5$ m.m. broad. The cells making up the walls were roughly cylindrical and 13 to 18 μ long and 13 μ wide. The aecidial 'horns' remained closed for many weeks. Fig.8.

It is interesting to note that as long ago as 1884 this 'abnormality' as it was called was seen and written about (Smith 1884). W. G. Smith observed the horned aecidia on material exhibited by Plowright, and stated that the aecidia 'look like little golden rods instead of shallow saucers.' Smith published a drawing with his account.

Such aecidial formations on the barberry have been noted many times since then. Mains (1924) mentions having seen them in his greenhouses at Indiana, and Prasada (1947) observed them in India. The still air which is usually present in greenhouses

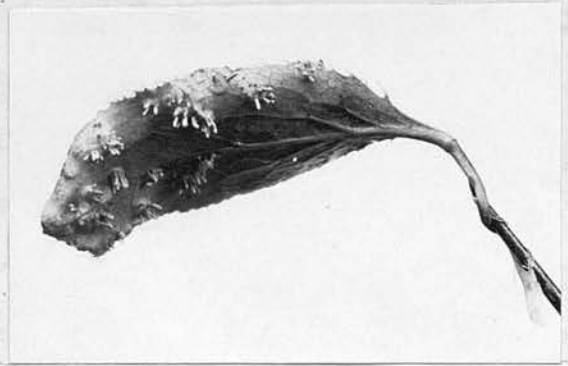


Fig. 8.

Barberry leaf with aecidial 'horns' formed
after artificial inoculation.

is probably responsible for the aecidia developing in this manner. Occasionally similar structures have been observed under natural conditions when an odd infected leaf has been growing in a sheltered position.

About the time these horns were first observed an interesting paper from Greece appeared (Critopoulos 1947). Its author reported finding uredospores and teleutospores naturally formed on Berberis cretica. This phenomenon was apparently linked with high temperatures and dryness of the atmosphere. These were the conditions existing in the writer's glasshouse when these horns were formed and as a matter of interest a search was made around the aecidia to see if any uredo or teleutospores had been produced. However, no such spores were found.

2. UREDOSPORES

(i) Germination

Much has been written on the germination of uredospores. Some of this work is referred to when considering meteorological conditions and the development of the rust. Here briefly will be stated the method used by the writer for germinating uredospores, more detailed results of which are included in the meteorological section already referred to.

When carrying out experiments on uredospore germination, results obtained by dusting the spores on the surface of water in a watch glass were not very satisfactory. The results fluctuated quite a lot and the actual percentage figure for germination was never very high. It was therefore felt necessary to look

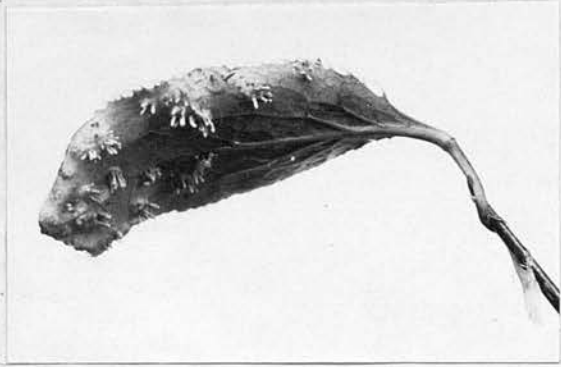


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around for some more suitable medium for germinating the spores.

The method which Loegering (1941) found satisfactory was adopted. He used 1% agar medium and results obtained by this means have been very satisfactory. Freshly formed uredospores dusted onto the surface of the agar in a watch glass have given over 95% germination.

(ii) Inoculation

The writer has been handicapped by the lack of suitable greenhouse accommodation. The only house available was one situated on the roof of the College. As can be imagined, the atmosphere during the summer months became very hot and dry. For the first season or so the results of inoculation experiments were very unreliable and few really successful inoculations were obtained. It was thought that the dryness of the atmosphere was perhaps largely responsible.

To try and correct this dryness, corrugated sheets were placed on the greenhouse benches and covered with a 2 inch layer of rather fine gravel. This gravel was kept moist and the humidity in the house was noticeably increased.

The method of inoculating plants with uredospores was as follows:-

Six seedlings were grown in compost in 6 inch pots. The first and second leaves were usually inoculated. The bloom was first removed from the leaves by gently passing them between the thumb and fore finger. The plants were then sprayed with

water and the appropriate uredospores applied to the leaves with a scalpel.

After inoculation the pots were labelled, stood in a shallow tank containing water and covered with bell jars for 48 hours. At the end of this incubation period the bell jars were removed. The pots were left standing in the water throughout the period of incubation and development.

Thus by having the pots standing in shallow water and also having the moist gravel on the benches the atmosphere inside the greenhouse was kept reasonably humid, even on the warmest days. By this means excellent results were obtained, and, during the summer and early autumn any plant which failed to become infected could fairly certainly said to be resistant.

Care was taken to protect each pot from outside infection, and if for any reason infected seedlings were to be kept after the result of the inoculation had been seen, then such seedlings would be covered with cellophane mounted on light metal frames so that spores could not blow about and perhaps bring about chance infection on other plants.

PART VII

A FUNGUS PARASITIC ON PUCCINIA GRAMINIS

When examining barberry bushes at one locality in mid Lothian on 22 July 1948, many of the aecidia present were seen to be covered with a sort of brownish scum. On taking such aecidia back to the laboratory it was obvious that the aecidia were parasitized by another fungus. It was identified as a species of Tuberculina (probably persicina). A search was made in the literature for reference to black rust being parasitized by this fungus, but apparently this is a new record, at least for naturally occurring infection.

A Russian worker (Vladimirskaya 1939) artificially inoculated the spermogonial and aecidial stages of black rust with T. persicina and obtained positive results after an incubation period of 8 days. This resulted in inhibition of further development of the rust. Negative results were obtained with inoculations of uredosori.

The parasite has been seen at only two localities, both of which are in mid Lothian. It appeared towards the end of July in 1948 and 1949, and arrested further spread of spores from infected aecidia. Not all the aecidia are infected on any leaf.

PART VIII

THE PHYSIOLOGIC FORMS OF PUCCINIA GRAMINIS
PRESENT IN S.E. SCOTLAND

1. HISTORICAL BACKGROUND

The historical aspect of our knowledge of the existence of physiologic forms within a species of rust has been dealt with fully in many papers published in recent years. Only a short account need, therefore, be given here.

The existence of well defined strains within a morphological species of rust was first demonstrated for Puccinia graminis by Eriksson and Henning at the end of the last century (Eriksson & Henning 1894, Eriksson 1894). Working in Sweden they showed that there were several of these strains, which were called by them formae speciales. Similar occurrences were identified about the same time in Kansas (Hitchcock & Carleton 1894).

Puccinia graminis has then been divided into the following physiologic forms:-

- (a) tritici on wheat
- (b) avenae on oats and certain grasses
- (c) secalis on rye and certain grasses
- (d) agrostidis on Agrostis spp.
- (e) poae on Poa spp.
- (f) airae on Aira caespitosa

To this list was later added epigaei on Calamagrostis spp. (Eriksson 1930).

In England Mehta (1923) in his experiments at Cambridge showed that two physiologic forms were present, tritici and secalis. In Scotland

Maxwell and Wallace (1926) found that five forms were present, namely tritici, secalis, avenae, phlei-pratensis, and agrostidis. It should be stated however, that in the latter paper the evidence put forward for the existence of the form phlei-pratensis is extremely slender.

2. THE FORMS FOUND DURING THE PERIOD OF THE PRESENT STUDY

(i) Materials and Methods

The host range of black rust in S.E.Scotland has been dealt with in a previous section (pages 13-20). It was indicated there that only slight infection has been found on a few of the grasses and it has therefore not always been possible to identify the physiologic form present. However, for most of the hosts experiments have indicated which form is carried by them.

During the summer and autumn of 1949 after the conditions suitable for infection had been created in the glasshouse, an intensive study was carried out on the relationship between the various cereal and grass hosts.

Results of this sort of work can be presented in many ways. If the experiments with each grass and cereal were dealt with individually it is thought that the description would be long and tedious. The results are given, therefore, in a more or less summarized form. By so doing it is thought that the relationships of grass and cereal infections can be more clearly understood. It should be stated that except where indicated, each inoculation was repeated

several times. For example with cereals four or five seedlings were grown in each pot and inoculated, and during the season many such pots of seedlings were used. With the grasses, several tillers per pot were inoculated and again several pots of each were used.

(ii) The Physiologic Forms

Experiments carried out chiefly in the 1949 season showed that the following physiologic forms are present in S.E. Scotland:-

	<u>Puccinia graminis tritici</u>	- Erikss. & Henn.
"	" <u>secalis</u>	- Erikss. & Henn.
"	" <u>avenae</u>	- Erikss. & Henn.
"	" <u>agrostidis</u>	- Erikss.
"	" <u>poae</u>	- Erikss. & Henn.
probably	" <u>phlei-pratensis</u>	- (Erikss. & Henn.) Stak. & Piem.

The natural hosts and results of inoculation experiments with each form are as follows:-

P. graminis tritici

natural host	- Triticum vulgare.
weakly infected by	- Hordeum vulgare, Secale
artificial inoculation	cereale.
inoculated but not infected	- Agropyrum repens, Agrostis spp., Anthoxanthum odoratum, Avena sativa.

P. graminis secalis

- natural hosts - *Agropyrum repens*, *Bromus sterilis*, *Hordeum vulgare*, *Secale cereale*.
- inoculated but not infected - *Agrostis* spp.,
Anthoxanthum odoratum,
Avena sativa, *Lolium italicum*, *L. perenne*,
Triticum vulgare.

P. graminis avenae

- natural hosts - *Alopecurus pratensis*,
Arrhenatherum avenaceum,
Avena fatua, *A. sativa*,
Dactylis glomerata,
Trisetum flavescens.
- easily infected - *Poa pratensis* (one test
artificially only).
- inoculated but not infected - *Agropyrum repens*,
Anthoxanthum odoratum,
Holcus lanatus, *Hordeum vulgare*, *Lolium italicum*,
L. perenne, *Phleum pratense*, *Secale cereale*,
Triticum vulgare.

P. graminis agrostidis

- natural hosts - *Agrostis alba*, *A. vulgaris*.
- inoculated but not infected - *Avena sativa*, *Hordeum vulgare*, *Secale cereale*,
Triticum vulgare.

P. graminis poae

natural hosts - *Poa pratensis*,
P. trivialis.
easily infected arti- - *P. annua*
ficially.
inoculated but not - *Avena sativa*, *Hordeum*
infected. *vulgare*, *Secale cereale*,
Triticum vulgare.

P. graminis phlei-pratensis

natural host - *Phleum pratense* (one
record only).

3. DISCUSSION

Studies on the physiologic forms of black rust present on cereals and grasses are reported in plenty in the literature. Certain features are more or less agreed upon by most workers, but there are many differences of opinion regarding certain minor points - only the more important work will be discussed in relation to the above results.

With P. graminis tritici Stakman and Piemeisel (1917) found that rye and some species of Agropyrum (other than repens) were natural hosts. The same workers were able to weakly infect A. repens and oats. They actually report being able to infect each cereal with almost every physiologic form. Nothing like this range of infection has been experienced by the writer, and it is thought that there were, perhaps, certain peculiar conditions existing in Stakman and Piemeisel's greenhouses that enabled the various forms to infect freely. Mehta (1923) was unable to infect rye, but did infect barley with P. graminis tritici.

Guyot and his colleagues at Grignon have done a considerable amount of work on the forms present on many species of grass. From their work it would seem that there occur on many grasses and cereals (grasses particularly) forms of black rust which are not readily classifiable into the formae speciales as generally accepted. Their results are therefore not strictly comparable with those of other workers, but where possible their results will be discussed.

Thus they (Guyot, Massenot & Saccas 1946) find barley to be equally susceptible to the wheat form, as also are two strains of rye.

The writer is in complete agreement with Stakman and Piemeisel in their conclusion that barley, rye and couch grass are natural hosts of P. graminis ^bseclis. The writer has been unable to infect wheat with this form. Stakman and Piemeisel weakly infected wheat, Mehta infected one variety, Red Sudan. The French workers consider the infections on rye and couch to belong to the same form, but separate the rust on Hordeum. They find that wheat is susceptible to the Hordeum form and in their 1945 report state that couch grass and rye isolates also brought about infection on wheat. This point is not mentioned in their 1946 report.

P. graminis avenae is the form which is of most importance economically. As far as host range is concerned it is also the most widespread.

Digressing for a moment, the possible reason why this form should be all important and most virulent in the area under review has been of some concern to

the writer. Variation in the virulency of various races within a physiologic form is a well known feature of the cereal rusts. Variation in the virulency of cultures assigned to a single race is also met with. Such variants are termed biotypes and were found to exist in a few yellow rust races isolated by Manners at Cambridge (unpublished data). Johnson (1949) reports biotypes of race 15 of P. graminis tritici. However, little or nothing appears to have been published on the possible variation in the virulence of various forms in an area. It may be that the climate favours P. graminis avenae in S.E. Scotland, as opposed to, for example, P. graminis tritici which is rarely met with, and even when it is, it only develops to a slight degree on any host. Obviously, further work is required along these lines.

Stakman and Piemeisel found P. graminis avenae occurring naturally on oats, the wild oat and cocksfoot, and could easily infect meadow foxtail and, strangely enough, Yorkshire fog.

Infection on the latter grass was always searched for. It usually grows in plenty near barberries, but has never been seen infected. Guyot and his colleagues could easily infect oats, tall oat grass, cocksfoot, golden oat grass and sheep's fescue with the avenae form. Festuca rubra, red fescue, has been seen bearing natural infection in Scotland and it has always been in association with infection on the other grasses just mentioned. It is, therefore,

highly probable that red fescue carries the avenae form. This grass is not given as a host of the avenae form by Stakman and Piemeisel.

P. graminis agrostidis is apparently confined to species of *Agrostis*. Similarly P. graminis poae is confined to species of *Poa*.

It is of interest to note that in one test, Poa pratensis was successfully inoculated with P. graminis avenae. It is, according to the literature, very unusual for a *Poa* sp. to be infected with any form other than Poae. There are, however, at least two records of P. graminis avenae being isolated from *Poa* species (Stakman 1914, Fischer & Claassen 1944).

References to black rust infection on sweet vernal grass are rather rare. In France it was observed (Guyot et al 1946) that isolations from the grass would not infect the cultivated cereals, as also has been the case with the Scottish material. Fischer and Levine (1941) indicate that the grass carries the avenae form. This has also been reported from South Africa (Verwoerd 1935) for *A. aristatum* - a closely related species - In Australia (Waterhouse) 1941) it was found that an Anthoxanthum odoratum isolate would not infect wheat or oats.

PART IX

A STATISTICAL STUDY OF THE UREDOSPORES AND
TELEUTOSPORES OF THE FIVE PHYSIOLOGIC FORMS OF
PUCCINIA GRAMINIS COMMONLY FOUND IN
S. E. SCOTLAND

1. HISTORICAL BACKGROUND

Levine (1923) was the first to apply a statistical study to the then known physiologic forms of black rust. He measured spores of the forms tritici, secalis, avenae, phlei-pratensis and agrostidis. A year later Stakman and Levine (1924) added the measurements of the form poae and in this paper the six forms were compared.

During recent years considerable work has been carried out at Grignon by Guyot and his colleagues who have examined and measured many thousands of uredo and teleutospores collected in many parts of the world. Table I is taken from one of the papers (Guyot et al 1946a) published by these French mycologists. Examination of this table will show the very limited differences which Guyot and his colleagues found to exist between certain samples and yet they consider these differences to be of sufficient importance to justify the making of new subspecies and varieties. Their classification obviously gives no indication of the relationship between, for example, cereal and grass infectivity. Using Guyot's terminology infection on Dactylis would be named P. graminis subsp. media var erikssoni and oat infection would be P. graminis subsp. major var. stakmani. No indication is given that the rust

TABLE I

THE SUB-DIVISION OF THE SPECIES PUCCINIA GRAMINIS PERS. (after Guyot et al 1946 a)

PUCCINIA GRAMINIS

Subspecies	Variety	Hosts	Formae speciales	Uredospore means	Teliospore means
Minor		Anthoxanthum Cynosurus		22 - 25 x 15 - 17	30 - 45 x 18 - 21
Media	erikssoni	Agrostis	agrostidis		
		Aira	airae		
		Alopecurus	aperae		
		Arrhenatherum	arrhenatheri	23 - 30 x 15 - 18	37 - 50 x 16.5 - 22
		Dactylis	? festucae		
Major	erikssoni	Festuca	? phleipratensis		
		Hordeum maritimum	? poae		
		Hordeum murinum			
		Calamagrostis	calamagrostidis	25.8 x 16.4	46 - 51 x 19.4 - 20.5
			epigeii		
Major	loli	Lolium		22 - 27 x 15 - 18	31 - 44 x 17 - 21
		Vulpia		23 - 26 x 15.5 - 18	47.5 x 20.7
	stakmani	Agropyrum			
		Avena	avenae	24 - 31 x 15 - 20	42 - 57 x 16 - 23
		Hordeum	hordii		
		Secale	secalis		
Major	tritici	Triticum	tritici	28 - 35 x 17 - 20	45 - 58 x 17 - 22
			tritici-compacti		
Major	elymi	Elymus		29 - 36 x 17 - 18.5	54 - 60 x 18.5 - 22.5

can be inoculated quite freely from the grass to the cereal and vice versa. Also the French terminology would be very cumbersome to use as the two examples just given demonstrate. With our present day knowledge the use of the old formae speciales is considered to be the best and most workable.

2. MEASUREMENTS OF SPORES

(i) Materials and Methods

In 1948 and 1949 material of the physiologic forms known to be present in S.E.Scotland was collected, the spores were measured and a statistical study applied to the measurements in much the same way as Stakman and Levine did for American material.

Uredo and teleutospores of the forms tritici, seclis, avenae, agrostidis, and poae were obtained on wheat (Triticum vulgare), bent grass (Agrostis vulgaris) and rough stalked meadow grass (Poa trivialis) respectively.

All the spores were measured with the same microscope and micrometer eyepiece. The microscope was fitted with a mechanical stage so that the slide was moved and no spore could be measured more than once.

Freshly collected uredospores were always used, care being taken to dust only mature spores onto the slide. Teleutospores were taken from material which had been stored in the laboratory about six weeks. The spores were always mounted in tap water.

100 uredospores of each form were measured and for reasons stated later, 200 teleutospores.

(ii) Results and Discussion

Table II contains the measurements of the spore forms. For interest and comparison Stakman and Levine's measurements are given in Table III.

(a) Uredospores

As far as the uredospores are concerned the measurements of the various forms collected in Scotland are very similar to those given by Stakman and Levine. P. graminis tritici has the longest, P. graminis poae the shortest spores. The avenae form is longer than the secalis form, the secalis is longer than the agrostidis form. The spore lengths of the five forms are significantly different from one another, a feature noticed also by the American workers.

Table III indicates that the spore widths of the American tritici and avenae forms are about equal, the latter being slightly broader. Secalis is more than 2 u narrower than either of these forms. The poae and secalis forms are about equal in width, but considerably narrower than any of the other forms. Of the Scottish material, tritici has the broadest spore followed by the avenae and secalis forms. Again the agrostidis and poae forms are about equal in width, both being considerably narrower than the other three forms.

The difference in width between the uredospores of the tritici and avenae forms is not significant, neither is that between the agrostidis and poae forms. The widths of the latter two forms are, however, significantly different from the widths of the forms

TABLE II

MEASUREMENTS IN MICRONS OF THE PHYSIOLOGIC FORMS COLLECTED
IN S. E. SCOTLAND

(The mean figure is given in each case)

Pysiologic form	Uredospores		Teleutospores	
	length	width	length	width
P.gr. tritici	30.52 \pm 0.34	18.12 \pm 0.19	48.79 \pm 0.35	17.84 \pm 0.12
P.gr. secalis	26.23 \pm 0.23	17.01 \pm 0.14	48.19 \pm 0.39	17.87 \pm 0.11
P.gr. avenae	28.69 \pm 0.35	17.72 \pm 0.24	47.27 \pm 0.36	17.62 \pm 0.13
P.gr. agrostidis	24.76 \pm 0.30	14.18 \pm 0.19	39.28 \pm 0.32	16.81 \pm 0.13
P.gr. poae	20.85 \pm 0.30	14.17 \pm 0.17	35.46 \pm 0.36	16.94 \pm 0.12

TABLE III

MEASUREMENTS IN MICRONS OF THE PHYSIOLOGIC FORMS COLLECTED
IN THE UNITED STATES

(Lévine 1923, Stakman and Levine 1924)

Pysiologic form	Uredospores		Teleutospores	
	length	width	length	width
P.gr. tritici	32.40 \pm 0.19	19.79 \pm 0.06	51.80 \pm 0.49	16.67 \pm 0.12
P.gr. secalis	27.14 \pm 0.14	17.19 \pm 0.06	47.35 \pm 0.45	14.77 \pm 0.12
P.gr. avenae	28.50 \pm 0.15	19.94 \pm 0.07	46.15 \pm 0.43	15.84 \pm 0.12
P.gr. agrostidis	22.37 \pm 0.12	15.68 \pm 0.05	40.30 \pm 0.40	14.64 \pm 0.12
P.gr. poae	18.64 \pm 0.10	15.78 \pm 0.07	36.90 \pm 0.62	15.52 \pm 0.14

tritici, avenae, and secalis. The secalis form has significantly narrower spores than either the tritici or avenae forms. There is exactly the results obtained by Stakman and Levine.

It can be seen by comparing both tables that the range in length of the five forms is not so great in the Scottish material as it is in the American. The latter forms are also somewhat wider than the former.

(b) Teleutospores

In general the measurements of the spores obtained from the two countries are similar. In many details, however, they are quite different. Bearing in mind the close similarity in the uredospore measurements obtained in the two countries it is rather surprising, although interesting, that the teleutospore measurements are rather different. Because of these differences, therefore, 200 teleutospores of each form were measured so that a reliable mean could be obtained. Both results show that the tritici form has the longest, and the poae form the shortest spores. In American material the difference in length between the forms tritici and seclis is considerable (4.45 u), while in material from Scotland it is only 0.60 u. On the other hand, the difference in length of the avenae and agrostidis forms is greater in Scotland than it is in America.

When comparing the widths of the teleutospores it is at once obvious that for each form the figures given for Scotland are considerably greater than those given for America. There is, however, a straight-forward reason for this. Stakman and Levine state

that they measured the width of the spores at the septum. The writer, on the other hand, took the broadest point for measuring, this usually being about the middle of the upper cell. Thus the two sets of figures given for teleutospore widths are not strictly comparable.

Considering the physiologic forms obtained in Scotland it can be seen that the differences in spore length of the various forms are most pronounced - the widths do not vary to any great extent i.e. there is only 1.06 μ difference between the narrowest (agrostidis form) and the broadest (secalis form). The American results do indicate that the agrostidis form is possibly the narrowest, and yet the secalis form is almost equally as narrow (at least at the septum).

Stakman and Levine state that the tritici form has significantly longer and wider teleutospores than either the secalis, avenae, or agrostidis forms. There is no significant difference between the lengths of the avenae and secalis forms, but their width differences are significant.

The secalis and avenae forms are significantly longer than the agrostidis form. The avenae form is significantly wider than the secalis form.

The poae form has the shortest spore and it is significantly so in all cases. The width of this form is stated to vary considerably and no statistical comparisons are given.

The results of the measurements of the forms collected by the writer are not always in accordance

with those given in the previous paragraph. The teleutospores of the tritici form are significantly longer than those of the avenae, agrostidis and poae forms, but the lengths of the tritici and secalis forms do not differ significantly, neither do those of the secalis and avenae forms. However, the lengths of the avenae, agrostidis and agrostidis poae forms are significantly different.

As already stated, the widths of the teleutospores of the five forms do not vary much. The tritici secalis and avenae forms are significantly wider than the agrostidis poae forms, but otherwise the differences between the widths of the various forms are not significant.

PART X

THE PHYSIOLOGIC RACES OF PUCCINIA GRAMINIS
AVENAE. ERIKSS. ET HENN.

1. HISTORICAL BACKGROUND

The composite nature of Puccinia graminis Pers. was first demonstrated in 1894 by Eriksson and Henning (1894) and Eriksson (1894). Further specialisation in P. graminis avenae was not shown until 1923 when Stakman, Levine and Bailey (1923) described four distinct physiologic races of this rust. These workers inferred the existence of a fifth race and Bailey (1925) described this. From further collections by Gordon and Bailey (1928) race 6 was described. Waterhouse (1929) then isolated two new races from Australia, race 7 (originally numbered 6) and race 8 (originally numbered 7). These two races were found also in Canada about the same time. Race 10 was discovered in 1930 in the United States (Cotter. 1932) and race 11 was first discovered in Germany seven years later Hassebrauk (1938). Race 12 was first seen in 1938 but was not described until 1944 as was also race 13 (Newton & Johnson 1944). This latter race was first obtained from aecidia on barberry artificially inoculated with race 3, but was later found in the field. A recent paper (Fischer & Classen 1944) gives an account of a possible fourteenth race, obtained from black rust collected on Poa ampla Merr. in the Washington area of America. However, there is a certain amount of dubety about its authenticity as all but one of seventeen varieties of oats inoculated have proved immune.

The early work on identification of the

physiological races of P. graminis avenae was carried out using the varieties White Tartar, Richland and Joannette Strain as the differentials. More recently the name White Russian has been given to White Tartar, and a re-selection of Joannette Strain called Sevnothree is now used.

2. IDENTIFICATION OF RACES IN S.E. SCOTLAND

(i) Materials and Methods

Early in 1949 seed of the three differential hosts was obtained from Canada through the generosity of Dr Craigie and Dr T. Johnson. During the season, samples of P. graminis avenae were collected from wherever possible in S.E.Scotland.

Seedlings of each differential host were raised in 6 inch pots and the inoculations were performed as described previously (page 33).

For the identification of the races isolated, the following table of infection types was used. This table is based largely on that given by Newton and Johnson (1944).

Explanation of symbols used in Table IV

- '0' - no pustules produced. Flecking may be present.
- '1' - A few very small isolated pustules, surrounded by sharply defined necrotic areas.
- '2' - Pustules small, usually isolated, surrounded by necrotic areas.
- '3' - Numerous medium sized pustules with a tendency to coalesce. A certain amount of chlorosis present.



TABLE IV

INFECTION TYPES PRODUCED ON SEEDLING LEAVES OF THREE
OAT VARIETIES BY 13 PHYSIOLOGIC RACES OF
PUCCINIA GRAMINIS AVENAE

(after Newton & Johnson 1944)

Race	White Tartar			Richland			Sevnothree			
	Range			Range			Range			
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
1	2-	3+	2+	0	1+	1	1-	2++	1 ⁺	
2	2=	3+	2++	1-	2+	1+	4=	4+	4	
3	3	4+	4-	1	2++	1	0	1	1-	
4	4-	4++	4	4-	4++	4+	0	1+	1	
5	1++	3+	2++	1-	2+	1++	1	X++	X ⁺	
6	4+	4++	4+	4+	4++	4+	4+	4++	4+	
7	3	4+	4	0	2+	2=	3	4+	4-	
8	0	2+	2	3	4+	4	3	4	3++	
9	2-	3+	2 ⁺	X=	4+	3++	3++	4++	4	
10	1	2+	2	3	4++	4	X-	X++	X+	
11	1	2+	2+	3	4++	4	1-	2++	1+	
12	4	4+	4=	1	2+	1++	X-	X++	X+	
13	3+	4+	4-	3+	4+	4-	X-	X+	X	

'4' - Pustules large, numerous and often confluent.

Only slight chlorosis present.

'X' - Pustules very variable. All infection types may be present on the same leaf.

(+) and (-) indicate quantitative variations in the type of pustules produced.

(ii) Results and Discussion

During the season 15 isolations were made from oats (14 collected in the Borders, 1 in Angus). The mean reaction on the varieties White Tartar, Richland and Sevnothree was 2+, 1-, and 1+ respectively in almost every case. Occasionally a reaction 2-, 1 and 1- was obtained. Referring to Table IV it will be seen that this reaction (2+, 1-, 1+) is characteristic of race 1. The other reaction (2-, 1, 1-) occasionally observed also of course fits in with race 1. Two isolates from Dactylis glomerata growing in widely separated places also gave the characteristic reaction of race 1.

It is surprising that with the large number of barberries present, offering endless scope for hybridisation, only the one race has been found on oats and cocksfoot. Mehta (1940) also comments on

the small number of races (of P. graminis tritici) which he found in India. He states 'Judging from the small number of physiologic races found so far, it appears that, as in Australia, the formation of new races as a result of infection on barberries in this country occurs very rarely, if ever.'

Uredospores obtained from Alopecurus pratensis however, collected in two localities in the Borders gave a mean reaction (several tests) of 2, 1, 3-, and 2, 1-, 2+, on the varieties in the order already given. Dr Johnson in private correspondence on the subject has indicated that race 2 may be present here. In the Table the minimum infection for race 2 on Sevnothree is 4-. Obviously further tests are required with spores from this grass.

During 1950 and later years it is proposed to carry out a survey of the whole of Great Britain to ascertain the races of P. graminis avenae present. South Scotland will demand particular attention, because the avenae form is all important there.

Note: Since the writer came to Cambridge a culture of black rust on oats was obtained from the Botany School. This has been put on the three differential varieties and the mean reaction has been 1+, 2+ and 3. Reference to Table IV will show that this reaction is nearest race 8. Doubtless under summer conditions each variety would be somewhat more susceptible and the reaction typical of race 8 would be obtained i.e. 2, 4, and 3++.

PART XI

THE REACTION OF OAT VARIETIES TO BLACK RUST
INFECTION IN THE FIELD AND THE EFFECT OF THE
RUST ON YIELD AND QUALITY OF THE GRAIN

1. INTRODUCTION

At the commencement of the present study, nothing was known in this country of the susceptibility or otherwise of the varieties of oat commonly grown here. In many other countries, perhaps Canada in particular, considerable research has been carried out on varietal susceptibility to black rust, and many resistant varieties, at least to certain races, have now been developed.

The losses brought about by this rust in other countries especially on the wheat crop have been stressed many times in the literature. However, as far as is known no work on the actual effect of black rust on oats has been carried out. As indicated previously P. graminis avenae is the important physiological form in S.E.Scotland and thus it was decided to attempt to ascertain the effect of infection on the oat crop.

For the purpose of the experiment a farm at Melrose was chosen the hedges of which contained a considerable number of barberry bushes. The experiment was conducted in two seasons (1948 and 1949) and for obvious reasons the plots were in different fields each season. A rough plan showing the relative positions of the oat plots in each season together with the nearest barberry bushes is given in Fig.9.

(1) Materia Fig. 9.

Diagram showing general position of plots in the two seasons.
 in plots 18 ft x 20 ft in the arrangement shown
 below. Fig. 9. The varieties used were mainly those
 recommended for growing under Scottish conditions.
 All the seed was dressed with a mercurial dust.

There was a pathway 8 feet wide between each

RIVER TWEED

Pasture

Position
1949
Plots

Position
1948
Plots

Sheep
Dipper

Barberries

2. THE 1948 EXPERIMENT

(1) Materials and method

Twelve varieties of oats were sown in triplicate in plots 18 ft x 20 ft in the arrangement shown below. Fig.10. The varieties used were mainly those recommended for growing under Scottish conditions. All the seed was dressed with a mercurial dust.

There was a pathway 2 feet wide between each plot. The plots were situated near the river Tweed, and on the leeward side of the main concentration of barberries. The nearest barberries were 20 yards away from Row A.. Because of the nature of the experiment it would have been better if the plots could have been sown nearer the barberry hedge, but a sheep dipper etc. at one corner took up a certain amount of land and thus if sown nearer the hedge, the plots could not have been arranged in three rows. Plots 1A, 1B and 1C were under trees.

The plots were sown on 11 and 12 March. $1\frac{5}{8}$ lb of seed was sown broadcast on each plot (equivalent to 5 bushels per acre), and then raked in, care being taken to avoid spreading the seed into the pathways between the plots.

As will observe from Fig.10 two plots of Star, Onward and Potato were placed next to each other. This was due to an unfortunate error at the time of sowing, and the plots were then not so randomly arranged as was originally intended.

The crop around the plots was also oats, variety Yielder.

The centre was visited each week and notes taken

on the development of the crop and disease.

(ii) Observations during the season

The oats began to break Fig.10 the beginning of

THE PLAN OF THE PLOTS AS SOWN IN THE 1948 EXPERIMENT

barberry bushes started to open. On 10 May spermatia

were plentiful on the now expanded barberry leaves,

RIVER

Plot 1	Victory	Sun II	Victory
2	Eagle	S.84	Sun II
3	Star	Onward	Potato
4	Star	Onward	Potato
5	Sun II	Victory	Star
6	Supreme	Primus	Yielder
7	Marvellous	S.84	Marvellous
8	Potato	Eagle	Supreme
9	Ayr Commando	Primus	Yielder
10	Marvellous	Supreme	Ayr Commando
11	Eagle	Ayr Commando	S.84
12	Yielder	Onward	Primus

Row A

Row B

Row C

"standard area design". In 1948 a different design was used, but this will be dealt with later (page 22).

It can be seen from this table that the plots towards the center of the row had become the worst affected by this date. They were the plots nearest to the source of infection, i.e. the barberry bushes in

on the development of the crop and disease.

(ii) Observations during the season

The oats began to braird at the beginning of April and at about the same time the buds of the barberry bushes started to open. On 10 May spermatia were plentiful on the now expanded barberry leaves, and about a week later small swellings appeared on the under sides of infected leaves which, by 24 May became mature aecidial cups.

Scattered uredosori were observed on the plots nearest the barberries on 12 July, by which time the ears of all varieties had shot. The variety Potato was the last to shoot, Primus being the first. During the next 14 days infection spread and developed on most of the plots.

Between 26 July and 2 August the weather was very warm and on the latter date many of the plots exhibited a reddish colouration which is so characteristic of rather severe uredospore development on the straw.

Table V gives some information on the condition and the percentage infection of each plot on 2 August.

The severity of the disease expressed in Table V as infection percentage was judged by using a diagram similar to that used by Grainger (1947) and called a "standard area diagram". In 1949 a different diagram was used, but this will be dealt with later (page 62)

It can be seen from this table that the plots towards the centres of the rows had become the worst affected by this date. They were the plots nearest to the source of infection, i.e. the barberry bushes in

Variety

Condition of Plants

TABLE V

Infection Percentage

CONDITION AND PERCENTAGE INFECTION OF PLOTS 2.iii.48

(a) Row nearest hedge.

<u>Variety</u>	<u>Condition of Plants</u>	<u>Infection Percentage</u>
Victory	very green	1
Eagle	" "	1
Star	rather green	1
Star	" "	1
Sun II	" "	5
Supreme	yellowing	10
Marvellous	" "	40
Potato	" "	40
Ayr Commando	" severe blasting	15
Marvellous	" "	5
Eagle	very green	1
Yielder	yellowing	1

(b) centre row

Sun II	green	1
S.84	green	1
Onward	rather green	1
Onward	" "	5
Victory	very green	20
Primus	severe blasting of ears	40
S.84	green	5
Eagle	very green	5
Primus	severe blasting	40
Supreme	yellowing	5
Ayr Commando	rather green	1
Onward	" "	0.5

the hedge. Generally speaking also, the ripening of the plots, i.e. yellowing, is closely linked with the amount of infection present. The feature was noticed again in 1949.

This really was the last useful observation which could be made on the plots. As stated previously, the plots were near the river Tweed and on the night of 12-13 August after about 72 hours of torrential rain severe flooding occurred and the plots were under 2 to 3 feet of water for twelve hours or so. When the water receded the oat plants were covered with a thick coating of mud and one or two plots, particularly under the trees near the river were entangled with flood debris.

However, the soil dried out remarkably well during the following ten days and it was decided to carry on with the experiment and to harvest the plots. Due to the coating of mud it was unfortunately not possible to measure the amount of infection at the time of cutting, but most of the plots were quite severely infected.

(iii) The method of harvesting and threshing of the grain

On 23 August after first cleaning up the pathways between plots, each plot was cut with an Allen-Scythe and stooked in the usual way.

Unsettled weather followed for several weeks and it was necessary to transport the stooks to a barn, each stook being appropriately labelled. Threshing commenced in mid October and it soon became obvious that the mice had contributed to the general

misfortune of the experiment. They had eaten a certain amount of grain particularly from those sheaves next to the barn floor.

Threshing consisted of beating the sheaves of each plot with sticks on the barn floor. The chaff etc. was removed from each lot of grain by means of a small electric threshing mill. The grain from each plot was then put into strong small canvas bags and beaten hard several times against a firm surface, and again winnowed. By this means a nicely trimmed sample was obtained.

The grain from each plot was then riddled to separate the 'firsts' and 'seconds.' Two standard riddles were used, 0.137 inch on top and 0.094 inch beneath. The firsts consisted of material collected between the two riddles, the seconds being made up of the few large grains which remained on the '137' sieve together with the material which passed through the '094' sieve.

(iv) Results

In view of the undoubted loss of grain which occurred between actually cutting the plots and weighing the grain obtained, it is unlikely that much significance can be attached to the figures for yield. The results of the yield obtained from each plot are given in Appendix 1.

Figures for each variety of the 1000 grain weight 1000 groat weight and percentage groat were obtained. For the sake of comparison, similar figures were obtained for samples of the varieties which had been grown in a healthy condition at Boghall. It is

appreciated that these figures are not strictly comparable with those of the diseased oats from Melrose. This point is further discussed in the 1949 experiment. However, the results for both healthy and diseased oats are given in Table VI. In every case it will be seen that the diseased oats gave a lower 1000 grain and 1000 groat weight, and also a smaller percentage groat than the healthy oats.

Tables VII and VIII are of further interest. They contain as well as the results already given in Table VI results obtained for the 1000 grain weight and percentage groat of varieties grown in different parts of Scotland, Craibstone, Aberdeenshire and Auchincruive Ayrshire. The results for these latter centres were obtained privately from Dr Sword. Examination of these tables will show that the diseased varieties have given a smaller 1000 grain weight and percentage groat than any of the healthy varieties (healthy in so far as they were not attacked by black rust).

This is as far as the 1948 results at Melrose can be taken. A fuller treatment is made in the 1949 experiment.

3. 1949 EXPERIMENT

The experiences of 1948 unfortunate and otherwise were borne in mind in the second season and several alterations were made. The following is an account of the experiment in 1949.

(1) Materials and method

Twelve varieties of oats were again sown, ten of them being the same as in 1948, but instead of

TABLE VI

Variety	Boghall			Melrose		
	<u>Healthy Oats</u>			<u>Diseased oats</u>		
	Grain Wt.	Kernel Wt.	% Kernel	Grain Wt.	Kernel Wt.	% Kernel
Marvellous	55.75	40.65	72	42.37	26.93	63
Onward	48.55	34.45	70	39.30	27.00	68
Eagle	44.05	32.85	74	35.46	25.30	71
Sun II	46.20	34.33	74	35.49	23.85	67
Star	46.55	34.23	73	38.15	25.85	67
Victory	51.37	38.05	74	37.10	24.75	66
Yielder	47.25	31.82	67	42.45	28.23	66
Ayr Commando	40.77	29.70	73	38.91	26.27	67
Potato	38.75	29.34	76	33.65	23.75	70
Supreme	40.00	28.05	70	38.95	25.40	65
S.84	not obtainable			34.66	23.61	68
Primus	not obtainable			42.65	30.10	70

THE 1000 GRAIN AND 1000 KERNEL WEIGHT AND PERCENTAGE
KERNEL IN HEALTHY AND DISEASED OATS.

TABLE VII
WEIGHT OF 1000 OATS

	Melrose	Graibstone		Auchincruive	Boghall
Variety	1948	1946	1947	1947	1948
Marvellous	42.37 gm	43.7 gm	44.5gm	45.4 gm	55.75
Onward	39.30	42.1	41.0	38.0	48.55
Eagle	35.46	37.3	37.7	34.5	44.05
Sun II	35.49	39.1	41.2	41.2	46.20
Star	38.15	41.0	39.3	37.1	46.55
Victory	37.10	37.3	39.0	43.4	51.37
Yielder	42.45	39.9	44.2		47.25
Ayr Commando	38.91	39.1	36.2	38.0	40.77
Potato	33.65	35.6	35.8	35.2	38.75
Supreme	38.95	-	-	37.0	40.00
S.84	34.66	35.0	39.3	42.3	
Primus	42.65	39.3	37.2	-	

Primus and S.84 which apparently are now rarely grown. Golden Rain and S.225 (now named Milford) were sown. The plan of the plots is given in Fig. 31.

The plots in 1949 were 18 feet by 18 feet with pathways between the plots as in 1948. In 1949 each variety was sown twice only, in a mixed manner.

TABLE VIII

PERCENTAGE GROUT IN OAT

Variety	Melrose	Craibstone		Auchincruive	Boghall
	1948	1946	1947	1947	1948
Marvellous	63	75	71	75	72
Onward	68	72	70	72	70
Eagle	71	74	74	74	74
Sun II	67	76	72	74	74
Star	67	74	73	76	73
Victory	66	78	74	75	74
Yielder	66	75	66	67	67
Ayr Commando	67	77	72	77	73
Potato	70	78	75	77	76
Supreme	65			73	70
S.84	68	71	72	72	
Primus	70	76	75		

of yields and quality.

Obviously the best plots were those which were similar plots of oats to the other plots. It was necessary to keep them healthy by the application of sulphur to the plots with sulphur. This, however, was not possible and a neighbouring farmer, who was not a member of the club, was known to have a small area of land in the middle of the plots.

Primus and S.84 which apparently are now rarely grown, Golden Rain and S.225 (now named Milford) were sown. The plan of the plots is given in Fig.11

The plots in 1949 were 12 feet by 16 feet with pathways between the plots as in 1948. In 1949 each variety was sown twice only, in a randomised manner. Only one plot of Potato could be sown however, as the seed was in short supply. An extra plot of Golden Rain made up the number of plots to twenty four.

The plots were sown broadcast on 21 March, the rate of sowing being equivalent to 5 bushels per acre as in 1948. All the seed was dressed with a mercurial dust. The plots this year were near the hedge (row A being as near the hedge as is usual on normally ploughed land.)

The crop in the rest of the field was also oats, variety Ayr Commando.

When considering the 1948 results the need was felt for knowledge of the yield and quality which could be obtained from healthy oats grown under similar conditions. In 1948 grain grown at Boghall was utilised for purposes of comparison, but such a procedure was not very satisfactory and comparisons of yields and quality hardly justifiable.

Obviously the best plan would have been to grow similar plots of oats in the same field and endeavour to keep them healthy by, for example, dusting the plots with sulphur. This, however, was not possible and a neighbouring farmer, on whose land no barberries were known allowed the writer to use a small area of land in one corner of a field. Plots

Thus, as plots could be RIVER sown in another part of the field, it was thought that this was the best

Row B	Row A
Potato	Victory
Eagle	Star
Sun II	Supreme
Onward	Golden Rain
Ayr Commando	Yielder
Star	Sun II
S.225	Ayr Commando
Yielder	Marvellous
Golden Rain	Onward
Supreme	S.225
Victory	Eagle
Marvellous	Golden Rain

were sown on 28 March in this field in exactly the same way as they had been sown near the barberries. Obviously if black rust became severe it would have soon spread the $\frac{5}{4}$ of a mile or so (which distance separated these latter plots from barberries) and measures would need to have been adopted to control the rust.

Thus, as plots could not be sown in another part of the field, it was thought that this was the best compromise - the two sets of plots as sown would experience the same growing conditions as far as the general environment was concerned, and the soil was reasonably similar also in the two fields.

For the sake of convenience the farm where the oat plots were sown up against the barberry hedge will be called Barberry Farm, the farm where no barberry was known (the hedges consisting mainly of hawthorn) will be called Hawthorn Farm.

As in 1948 regular observations were made on the plots during the 1949 season.

(ii) Observations during the 1949 season

On 11 April the oats at Barberry Farm were brairding and the barberry buds beginning to open. Spermatia did not appear in any quantity until the end of May. By the middle of June aecidiospores were being discharged at which time the oats were on the average about 14 inches high. On 30 June the ears of most of the varieties had shot. Star and Yielder were somewhat later than the rest, except for Potato the ears of which were still enclosed in the leaf sheaths.

At Hawthorn Farm the oat seedlings were one to two inches high on 21 April. About a month later the plots were found to have been badly eaten by rabbits. An interesting feature was that the two plots of S.225 had come in for special attention and were very seriously eaten off. However, by 12 July all varieties had shot and it was observed that even in the S.225 plots several plants had headed.

On 12 July scattered uredosori were observed on the plots at the other farm, particularly on those plots nearest the barberry bushes. Sori were present on the internodes, outer glumes and rachises of scattered plants.

Mildew (Erysiphe graminis) was fairly severe on most plots at this time, particularly on the lower leaves. Numbers of these leaves were withering due partly also to the drought which had developed.

In 1948 Grainger's 'standard area' diagram was used for assessing the disease intensity of each plot. In 1948 a paper was published from Canada (Peterson, Campbell & Hannah 1948) which gave details of work on disease measurement especially connected with cereal rusts. In their scale the diagram representing 37% of the total surface being covered by rust pustules was selected as 100% infection. This procedure was based on the fact that mycelial development is more extensive than pustule development. The assumption was made therefore, that when 37% of the surface was covered with pustules, the development and destructiveness of the underlying mycelium are almost at a maximum. To support this the

Canadian workers measured the area of pustules on parts of plants killed or badly damaged by rust and they found that the rust areas did not exceed 37% of the surface.

In the field it was found that these Canadian diagrams were easier to use than Grainger's, and so throughout 1949 were adopted for general use.

Table IX gives an indication of the condition of the plots and amount of infection present on 29 July.

From this table and from Fig.9 it may be seen that the plots nearest the barberries were by far the most severely infected and were ripening more rapidly than less infected plots of the same variety. The straw of several of the more severely attacked plots was very brittle and was breaking over in the wind.

It was interesting at this time to note particularly in the worst affected plots, how many sori were present actually on the panicles of the oats. In nearly every case a sorus was present at the point where each spikelet arises from its pedicel. Most of the branches of the panicle also bore sori.

Although sown only a week later the plots at Hawthorn Farm were, except for Supreme, all very green on 29 July. It was obvious the way that black rust infected plants ripened much more quickly than uninfected plants. The healthy plots were cut on 19 and 24 August, Onward, Eagle, Star and S.225 not being quite ready for cutting on the former date. At the time of cutting a few uredosori were beginning to appear on these plots.

TABLE IX

CONDITION OF PLOTS AND AMOUNT OF INFECTION 29.vii.49.

(a) row against hedge.

<u>Variety</u>	<u>Condition of plots</u>	<u>Infection percentage</u>
Victory	green	1
Star	green	1
Supreme	yellow	1
Golden Rain	green	5
Yielder	"	5
Sun II	"	5
Ayr Commando	yellowing. straw brittle	20-40
Marvellous	"	20-40
Onward	"	20-40
S.225	rapidly ripening	80 *
Eagle	" "	80 *
Golden Rain	" "	80 *

* mainly teleutosori.

(b) row away from hedge.

Potato	green	1
Eagle	green	1
Sun II	yellow	1
Onward	"	5
Ayr Commando	"	10
Star	greener than Ayr Commando	5
S.225	yellowing	15
Yielder	"	15
Golden Rain	ripening	15
Supreme	"	20
Victory	not quite so ripe	40
Marvellous	" "	40

Most of the diseased plots were quite ready for cutting by 9 August. Five plots, namely Star, Victory, and Sun II, Eagle, Potato at the river end of rows A and B were cut 19 August.

(iii) The method of harvesting and threshing out of grain

In 1948 considerable work was entailed in harvesting the whole of each plot, tying into sheaves and stooking and then because of subsequent bad weather, labelling each sheaf and transporting all the sheaves to a barn. A certain amount of grain was lost while transporting to the barn, mice ate grain and altogether the experimental error must have been considerable. With such a large number of sheaves also, threshing out and subsequent riddling took several weeks of work.

With all this in mind it was decided in 1949 to just sample each plot. The plots were sampled by cutting 250 straws at random from each plot and then placing the produce from each plot immediately into a linen bag which was brought back to the laboratory, and hung up to dry in an airy place.

When cutting for sampling, the straw was severed a few inches above ground so that the usual length of straw remained beneath each panicle as in binder cutting. As each plot was sampled the percentage infection was estimated using the key given by (Peterson, Campbell & Hannah 1948).

There are undoubtedly drawbacks in the method just described, but as all the grain from the 250 heads was secured immediately, a certain amount of

reliance could be placed on the yield obtained.

Each plot was sampled at Barberry Farm, but one plot only of each variety was sampled at the other farm.

Each sample was left to dry for the same length of time, i.e. the plots sampled a week later were left hanging a week longer than the earlier cut plots - all plots being left about five weeks.

The grain was removed by hand from each sample. The chaff etc. was blown away by using a small electric blower. The grain was then beaten in small bags as in 1948 and the fine dust blown away so that a nicely trimmed sample was obtained.

The same riddles (137 and 094) were used again in 1949 to divide the grain into 'firsts' and 'seconds' which were then weighed.

(iv) Results

(a) Effect on grain yield

Table X gives the yield and percentage seconds of all the sampled plots together with the percentage infection of the rusted plots. For the diseased plots the lesser infected is given first.

Examination of this table shows that generally speaking the yield is inversely proportional to the severity of attack. This is shown particularly well with the varieties Victory, Sun II, Ayr Commando, and Marvellous. These are discrepancies of course, as would be expected in any small scale experiment of this

TABLE X

THE YIELD (GMS), PERCENTAGE INFECTION OF DISEASED PLOTS,
AND PERCENTAGE 'SECONDS' IN EACH PLOT SAMPLED IN 1949

Variety	Hawthorn Farm		Barberry Farm					
	Yield % 2nds		Row away from hedge			Row against hedge		
			Inf.%	Yield	% 2nds	Inf.%	Yield	% 2nds
Victory	19	6.5	100	16	35.9	1-20	17 $\frac{3}{4}$	26.7
Star	16 $\frac{1}{4}$	13.8	5-30	18	23.6	5-20	20 $\frac{3}{4}$	24.0
Supreme	17 $\frac{3}{4}$	4.2	40-80	19 $\frac{1}{2}$	14.1	1-20	19 $\frac{1}{4}$	12.9
G. Rain	19 $\frac{3}{4}$	32.9	10-50	13 $\frac{5}{8}$	58.1	1-10	20 $\frac{3}{4}$	56.6
Yielder	20 $\frac{3}{4}$	6.0	1-40	19	13.1	5-30	18 $\frac{1}{2}$	19.4
Sun II	23	13.0	1-10	18 $\frac{5}{8}$	34.6	40-70	18	36.1
Ayr Comm.	23 $\frac{1}{4}$	15.0	5-40	20	40.0	40-60	18 $\frac{3}{4}$	34.6
Marvellous	24 $\frac{5}{8}$	6.0	60-100	19 $\frac{5}{8}$	18.9	40-90	20	17.5
Onward	22	4.7	5-20	23	18.5	90-100	21 $\frac{1}{2}$	32.5
S.225	10 $\frac{1}{2}$	16.6	40-70	10 $\frac{3}{4}$	23.2	100	13 $\frac{1}{2}$	44.4
Eagle	13 $\frac{1}{4}$	32.0	1-20	18 $\frac{1}{2}$	41.8	100	16 $\frac{1}{2}$	62.1
G. Rain	19 $\frac{3}{4}$	32.9	10-50	13 $\frac{1}{4}$	58.1	100	19 $\frac{1}{2}$	71.8
Potato	17 $\frac{1}{4}$	18.8	1-30	13 $\frac{1}{2}$	24.0			

percentage seconds in the three samples of each variety will show that the same pattern is followed in every case except for the variety Ayr Commende. The more severely the plants are attacked, the greater is the amount of small grain, i.e. seconds, in the resulting yield.

Thus an attack of black rust on oats reduces the

kind. The varieties Star, Eagle, Supreme and S.225 have yielded better in the diseased than in the healthy plots. The three Onward samples have yielded roughly the same.

Omitting Supreme, these last named varieties have, however, something in common - they were the last to be harvested at Hawthorn Farm. Conditions were probably unfavourable there for their proper development, and the ears did not fill properly. Star, Eagle and Onward have, nevertheless, followed the same general pattern of yield, being proportional to the severity of attack.

Supreme was the earliest maturing variety sown, and thus would have been the furthest developed when the rust attacked. Thus it is possible that the rust came rather too late to affect the actual yield of grain.

The fact that some of the diseased plots, particularly when only slightly affected yielded as much or sometimes more than the healthy plot of the same variety, is surely quite a good indication that it was the rust infection which was responsible for reducing the yield.

Examination of the figures relating to the percentage seconds in the three samples of each variety will show that the same pattern is followed in every case except for the variety Ayr Commando. The more severely the plants are attacked, the greater is the amount of small grain, i.e. seconds, in the resulting yield.

Thus an attack of black rust on oats reduces the

actual yield and also produces a larger amount of small unwanted grain.

(b) The effect on grain quality

As is well known, the oat grain can be divided into two parts, the husk (made up of the lemma and palea) and the groat. In assessing the milling value of a variety the first essential is a high percentage of groat in oat. In the preparation of oatmeal the husk must be completely removed from the groat and so the miller requires as high a percentage of groat as possible. The husk is useless except as a constituent of low quality feedingstuffs. In this experiment most of the varieties grown are recognised as normally producing grain of good milling quality e.g. Victory, Star, Onward Eagle, Ayr Commando, Golden Rain and Potato.

Thus it is important to know the effect, if any, of black rust on the percentage groat in these varieties. Thus the 1000 grain weight, 1000 groat weight and then the percentage groat was ascertained for the three harvested plots of each variety. For this, the 1000 grains were randomly chosen from the firsts i.e. grain over the 0.094 inch sieve.

Before proceeding to give the results it is felt that a few remarks on 1000 grain weight, 1000 groat weight and percentage groat would not be out of place. The figures given for these values for each variety are fairly constant, but they do vary somewhat from season to season and with local conditions in any one particular season. The figures for 1000 grain weight will also of course, vary according to what riddles

have been used for obtaining the grade from which the grains have been taken. Two interesting papers (Sword 1948, Sword 1949) contain figures for the 1000 grain weight and percentage groat obtained in two seasons and at two centres (Craibstone in Aberdeenshire and Auchincruive in Ayrshire) for most of the varieties under consideration. These figures for four randomly chosen varieties are given in Table XI. It gives an indication of the sort of variation experienced.

Thus because of the considerable variation between one season and another and from centre to centre it is considered unsatisfactory to compare the figures obtained in the present study with similar figures obtained elsewhere and in different seasons.

In Table XII are given figures for the percentage infection, weight per 1000 grains and 1000 groats and the percentage groat in oat for each plot sampled. The results for each plot of each variety are given in the order of increasing rust attack, i.e. the left hand column consists of the healthy plots from Hawthorn Farm. There is much to comment on and discuss in this table and for convenience it will be dealt with under the following headings:-

weight per 1000 grains

weight per 1000 groats

percentage groat in oat

TABLE XI

THE 1000 GRAIN WEIGHT AND PERCENTAGE GROAT OF OAT SAMPLES
COLLECTED AT TWO CENTRES IN TWO SEASONS

Variety	Weight of 1000 grains			Percentage groat		
	Craibstone		Auchincruive	Craibstone		Auchincruive
	1946	1947	1947	1946	1947	1947
Onward	42.1	41.0	38.0	72	70	72
Star	41.0	39.3	37.1	74	73	76
Victory	37.3	39.0	43.4	78	74	75
Eagle	37.3	37.7	34.5	74	74	74

Weights in grammes.

TABLE XII

THE WEIGHT PER 1000 GRAINS, WEIGHT PER 1000 GROATS AND PERCENTAGE GROAT OF ALL PLOTS SAMPLED IN 1949. THE PERCENTAGE INFECTION IN RUSTED PLOTS IS ALSO GIVEN

Variety	Hawthorn Farm			Barberry Farm			
	Wt/1000 grain	Wt/1000 groat	% groat	% Inf.	Wt/1000 grain	Wt/1000 groat	% groat
Victory	45.70	33.22	72.6	1-20	44.37	32.01	72.1
Star	44.18	33.09	74.9	5-20	44.62	32.69	73.2
Supreme	44.77	32.67	72.9	1-20	42.13	29.00	68.8
Golden Rain	43.20	31.44	72.7	5-10	44.47	32.49	73.0
" "							
Yielder	50.93	35.11	68.9	1-40	46.90	32.40	69.1
Sun II	45.39	33.74	74.3	1-10	45.33	33.17	73.1
Ayr Commando	42.53	31.67	74.4	5-40	42.88	30.94	72.1
Marvellous	51.92	37.93	73.0	40-90	48.64	34.17	70.2
Onward	49.18	35.42	72.0	5-20	42.14	29.24	69.5
S.225	46.21	36.13	78.1	40-70	44.07	34.04	77.2
Eagle	41.45	30.52	73.6	1-20	42.81	31.59	73.7
Potato	39.49	29.91	75.7	1-30	38.47	29.39	76.3

Weights in grammes.

Weight per 1000 grains

For almost every variety, the 1000 grain weight is lower in the sample from the diseased plots. In most cases the weight is least in the plot with the greater infection. The varieties Victory, Sun II, Marvellous, and S.225 are typical in this respect.

In one or two slightly infected plots, e.g. Eagle Star and Golden Rain, with 1 to 20, 5 to 20 and 5 to 10 per cent infection respectively the 1000 grain weight figure is as high or even higher than the figure for the healthy plots. This, it is thought, is an indication that it is not a poorer soil or any other such factor which is responsible for the reduced 1000 grain weight of most of the diseased samples. The black rust infection itself is almost certainly the cause of smaller grain weight.

Weight per 1000 groats

As would be expected, this figure follows the same general pattern as that of the 1000 grain weight. The weight per 1000 groats generally decreases with a greater rust intensity.

Percentage groat in oat

Sword (loc. cit.) considers this to be a very important figure, of more value than either of the above two figures. As mentioned in a previous paragraph, all the best milling oats have a higher percentage of groat. Table XII demonstrates very clearly that an attack of black rust reduces this percentage, and the more severe the attack, the greater the reduction. Thus, for example, in this experiment a severe attack on Victory, Golden Rain,

Marvellous, Onward and Eagle, reduced the groat to below 70%. Such samples would be immediately rejected by the miller. It can be calculated from the figures in the table that in this experiment severe infection (about 100%) causes an average reduction in percentage groat of about 5%.

(v) The growing period of the host and the effect of black rust

The weather in the spring of 1949 was quite satisfactory from an agricultural point of view and cereal crops were sown in good time, if anything earlier than usual.

Likewise the summer was good and harvesting started early and farmers were able to complete their work without really a single day being lost because of bad weather.

On the other hand, the rust, as already indicated was very sporadic in its appearance and in most places particularly the Border counties was definitely quite late in 'getting under way.'

The growing crops were therefore exposed to rust attack for a comparatively short time. The first uredosori were observed on the plots at Barberry Farm Melrose on 12 July. On 9 August the plots were cut. Thus the oat plants were only exposed to the rust for four weeks. If the rust had appeared earlier and weather conditions were not quite so favourable for the crop so that the harvest was later, the results obtained at Melrose would undoubtedly have been quite different. The reduction in yield and quality of the grain from the diseased plots would almost certainly

have been more marked when compared with the results obtained from the healthy plots.

4. GENERAL CONCLUSIONS

The experiments carried out by the writer on the varietal susceptibility of oats to black rust, and the effect of the rust on the yield and quality of grain were of necessity on a small scale. Any field experiment entails a considerable amount of work, especially at the beginning and end of the season. Where most of the work has to be done by one person, therefore, the scale of the experiment must be kept within manageable proportions. Even so, however, the results presented in the foregoing pages do indicate that Puccinia graminis can be a serious menace to cereals, particularly oats, in S. E. Scotland.

In the actual seasons when experiments were carried out the rust was not particularly serious or widespread. But as the figures have shown, reductions both in yield and quality of grain were brought about. If a similar experiment could have been arranged during the 1947 season, when the rust was so widespread and severe, it is highly probable that far more significant figures would have been obtained for the reduction in yield and quality of the grain of oats.

Oat straw is also very necessary in the economy of the farm. It is superior to all other cereal straws in palatableness and nutritive value, and is largely used in place of hay for the winter feeding of stock. Rusted straw is extremely brittle and very unpalatable, as indicated by many farmers with

whom the writer has discussed the subject.

A rather badly rusted crop of Yielder oats was seen in Berwickshire in August 1949. The straw being brittle lodged easily in the wind and the panicles of many straws had actually broken off and were lying useless on the ground. Blackened headless lengths of straw were thus present in the crop poking up amongst other tillers, the heads of which were still present though rather poorly filled.

Another important result of the experiments just described concerns the susceptibility of the varieties grown to the rust. All the fourteen varieties used are susceptible to the rust, and as far as could be ascertained, equally so. From these and other observations made on various farms, no variety grown in this country is resistant to the rust. The only control of the disease, therefore, lies in the eradication of the barberries, as farmers cannot be recommended to grow resistant varieties. In several other countries oat varieties have been bred which are resistant to the rust. Except perhaps in S. E. Scotland the disease is not of sufficient importance in Great Britain to warrant a plant breeding programme aimed at obtaining oat varieties resistant to black rust.

THE INCIDENCE OF THE RUST EACH SEASON AND ITS
RELATIONSHIP TO THE METEOROLOGICAL CONDITIONS
OBTAINING DURING ITS ACTIVE PERIOD
i.e. APRIL-SEPTEMBER

1. GENERAL BACKGROUND

In section III it was indicated that the common barberry is found in plenty in S. E. Scotland, particularly in the Border counties. From the amount of barberry present one might expect black rust to be widespread each season. However, it has been stated that in most seasons the disease is confined to within a matter of yards of the source of infection. In certain years, though, the disease becomes severe and widespread, attacking cereals and grasses miles away from infected barberries.

From the earliest records of the disease one reads of severe attacks being accompanied by a warm humid atmosphere. Several of Sir John Sinclair's correspondents drew attention to this fact. More recently the influence of meteorological conditions on the development of black rust has been carefully studied in several parts of the world. It was thought worth while to investigate the possible relationship between meteorological conditions and the development of the disease in S. E. Scotland.

For this purpose the reports of seven meteorological stations in S. E. Scotland were examined for the years under review i.e. 1945-9. It is appreciated of course, that examination of five seasons only would not enable one to draw any definite conclusions from the results obtained, but it was thought that certain trends would perhaps be

indicated

(1) The meteorological stations

The following are the stations from which records have been taken. A few notes are given with each station together with the reasons for its choice.

(a) Leuchars, Fife - a coastal observatory, telegraphic reporting station, and so run by R.A.F. personnel efficiently supervised.

(b) Cupar, Fife - an inland station fairly representative of the conditions in Angus and Fife.

(c) Boghall, mid Lothian - a crop weather station, frequently checked by the writer.

(d) North Berwick, East Lothian - a coastal station but no suitable station exists inland in this county.

(e) Marchmont, Berwickshire) - Inland stations, records taken by private individuals.

(f) Kelso, Roxburghshire) - Fairly representative of the Border counties.

(g) Eskdalemuir, Dumfriesshire - an inland observatory just outside the actual area of investigation, but being a first class station its records have been utilised. Also fairly representative of the Border climate.

The stations selected do then quite well cover S. E. Scotland.

(ii) The years under review

Throughout this section the years under consideration are 1945-9. The incidence of the disease in each season has been given in a previous section, but for the sake of convenience a summary is given here.

The disease in 1945 - severe

" " " 1946 - slight

" " " 1947 - severe (most severe attack of all)

" " " 1948 - slight

" " " 1949 - moderate. Slight early in the season, developing later.

Thus in the following account the years 1945 and 1947 are grouped together as years of severe rust attack, 1946 and 1948 years of slight attack and 1949 is rather an intermediate year.

The purpose of this section is therefore to investigate the meteorological conditions obtaining during the active period of the rust i.e. April to September in these years and to ascertain if there is any similarity in the conditions existing in the years of severe attack and then to compare any such conditions with those obtaining in the other classes of rust attack.

(iii) The treatment of the subject

The meteorological conditions are divided up into humidity, temperature, light, and are considered separately under the headings given in the list of contents.

The references in the literature to the requirements for the various spore forms of moisture, temperature, etc., for germination, infection and subsequent development are very numerous. In 1945 a very comprehensive paper reviewing up to that date the literature on the physiology of the spore forms and weather relationships of the disease was published by Dr Craigie (Craigie 1945). In the following account the writer has therefore only given those references which are of direct relationship to the subject under discussion and has not given strings of literature references which all give more or less the same information. Dr Craigie's paper is undoubtedly the most comprehensive yet published on the epidemiology of black rust and to facilitate comparisons etc., the writer has followed Craigie's treatment of the problem

2. RELATION OF HUMIDITY TO THE DEVELOPMENT OF BLACK RUST

Sufficiency of moisture is essential for the establishment of infection of black rust which consists firstly of spore germination and penetration by the resulting germ tube into the host tissues. For spore germination and infection a film of moisture must be present around the spores. Stock (1931) obtained no germination at 90, 95, or 99% relative humidity and very little at 100% when no water condensed on the spores. It is, however, very difficult to work at relative humidities approaching saturation as the slightest change in temperature brings about immediate condensation on any solid

particles such as the rust spores.

To obtain infection with uredospores under greenhouse conditions liquid water must be present on the plants, and this condition must persist for a number of hours. It is almost certain that the same conditions will be necessary under natural conditions. When carrying out inoculations most workers leave the plants in a moist chamber for 48 hours. Peltier (1925) in a series of experiments inoculated seedling plants and kept them in moist chambers for varying periods of time. Less than 2% of the plants became infected when kept in the chambers for less than 5 hours, about 50% became infected from 18-20 hours, and 100% infection after 36 hours or more in the chamber. Thus the longer the optimum conditions for infection exist, the more uredosori will be produced.

(i) Amount of rainfall

Observations over a number of years in many parts of the world have tended to confirm the general opinion that wet seasons are usually seasons of severe black rust infection. In Australia Thomas, Samuel and Millington (1947) and Cass Smith (1948) draw attention to the fact that severe epidemics of black rust of wheat followed heavy summer rains. Rutti (1946) makes a similar statement for the conditions in Switzerland.

There are some workers, however, who state that black rust infection is not always most severe in seasons of highest rainfall. Lambert (1929) for example could find no correlation between heavy rainfall from May to July and the intensity of black rust

epidemics.

Roussakov (1923) makes the interesting point that too much importance is generally attached to the total rainfall in a given period. He regards the duration and frequency of the rains as being an important factor. Rain at night he considers very favourable for the spread of infection. Short storm showers are not favourable because they wash the spores off the plants. Peltier (1933) in Nebraska found that the lack of an even distribution of precipitation is the major limiting factor in the further development of the disease after primary infection.

To determine the extent to which seasonal rainfall is associated with the severity of black rust attack, rainfall data for the meteorological stations mentioned earlier have been assembled and are presented in Table XIII. As will be observed the months are grouped into May June, when the aecia may be said to appear and infect neighbouring cereals and grasses, and July August when the uredospores develop and spread the disease further afield.

This table shows that in most cases the May and June rainfall is greater in the severe rust years (1945 and 1947) than in the other years when the rust was very slight. The year 1948 provides the exception at one or two stations. The July and August rainfall for the slight rust years is in every case considerably more than the preceding May June rainfall. In many cases it is about double. When the years of severe infection are examined, however, the July August

TABLE XIII

TOTAL RAINFALL IN INCHES FOR FOUR MONTHS AT EACH STATION

			1945	1947	1946	1948	1949	Average
Leuchars	May	June	5.99	6.81	3.84	6.02	2.2	-
	July	August	6.62	2.07	5.45	7.22	6.0	-
Cupar	May	June	6.35	6.84	5.25	7.04	2.99	
	July	August	6.49	2.22	8.90	6.43	5.23	
Boghall	May	June	6.94	5.80	4.05	7.46	4.0	
	July	August	7.10	3.79	9.06	ex	5.6	
N. Berwick	May	June	5.98	6.47	4.69	3.86	3.11	3.65
	July	August	5.11	1.99	6.16	8.89	3.97	5.74
Marchmont	May	June	7.12	6.16	2.85	5.44	2.98	4.78
	July	August	6.01	2.85	6.48	11.13	4.87	6.36
Kelso	May	June	6.27	7.19	3.15	5.72	2.22	4.04
	July	August	4.13	3.09	7.25	11.59	4.56	5.58
Eskdalemuir	May	June	11.32	8.45	7.72	8.70	4.60	6.45
	July	August	5.93	4.53	10.83	13.83	6.31	9.25

ex = exceptionally heavy.

As might be expected the number of days when rain falls is closely correlated with the total amount of precipitation. Generally speaking there is a greater number of rain days in April, May and June in years of severe rust than in years of slight rust. Also the number of rain days in July August is considerably less in rust years. Therefore for a black rust epidemic in S. S. Scotland frequent rainfall is necessary in spring and early summer, with drier

rainfall is in most cases considerably less than the May June rainfall. In 1945 the Boghall Cupar and Leuchars rainfall was slightly greater in the first two months. In 1947 which was the year of severest rust attack, the July August rainfall was everywhere very considerably less than the May June rainfall. The rainfall in April gives little indication of the type of rust year to follow.

Thus for a severe attack of black rust heavy rainfall is necessary in late spring, to be followed by only moderate amounts. This is not quite in agreement with Craigie (loc. cit.) who found that the excess rainfall in the heavier rust years was distributed over the five month period April to August.

- ii Frequency of rainfall: As mentioned in a previous paragraph the frequency of the rainfall is quite as important as the actual amount which falls. The number of days when there was some precipitation (.01 inches or more) has been ascertained from the records of the seven stations. Table XIV gives the results in a somewhat summarized form.

As might be expected the number of days when rain falls is closely correlated with the total amount of precipitation. Generally speaking there is a greater number of rain days in April, May and June in years of severe rust than in years of slight rust. Also the number of rain days in July August is considerably less in rust years. Therefore for a black rust epidemic in S. E. Scotland frequent rainfall is necessary in spring and early summer, with drier

conditions following.

TABLE XIV

MEAN NUMBER OF DAYS WITH .01" OR MORE RAINFALL IN THE MONTHS APRIL TO AUGUST

		1945	1947	1946	1948	1949
Leuchars	April	9	16	4	9	11
	May June	37	37	31	35	26
	July August	23	13	35	35	23
Cupar	April	13	17	5	9	12
	May June	33	38	33	37	25
	July August	25	12	39	34	26
Boghall	April	16	20	10	14	20
	May June	44	40	34	40	38
	July August	36	13	45	39	34
N. Berwick	April	12	14	3	23	14
	May June	36	37	30	30	20
	July August	22	13	32	27	25
Marchmont	April	13	20	13	13	15
	May June	41	41	29	33	26
	July August	29	18	42	34	23
Kelso	April	15	19	11	11	14
	May June	39	41	30	34	21
	July August	29	21	33	33	21
Eskdalemuir	April	15	24	12	18	21
	May June	44	44	32	31	26
	July August	27	22	46	34	24

conditions following.

(iii) Duration of rainfall

The Eskdalemuir records give the number of hours during which rain fell and the results are brought together in Table XV.

It can be seen that the duration of rainfall from April to June is greatest in the severe rust years. Then in these years the duration in June and July is relatively small.

(iv) Occurrence of mist and fog

It is extremely difficult to record the occurrence of mist and fog and no suitable figures are available. When of course they are present, the vegetation would become covered with moisture making conditions ideal for spore germination and infection to take place. It is not possible to assess the importance of these phenomena in the development and spread of the rust.

(v) Relative humidity of the air

Although there has been a considerable volume of work published on the relation of weather conditions to the development of black rust, only a relatively few papers contain references to the relative humidity of the air. This, however, bears no relation to its importance as black rust spores depend on the presence of moisture for germination. The references which are made, however, are somewhat conflicting. This may be because of the difficulty in keeping accurate records. As is well known the relative humidity of the air changes from hour to hour, depending on the amount of water vapour present and the air temperature. As far

TABLE XV

DURATION OF RAINFALL IN HOURS AT ESKDALEMUIR

	1945	1947	1946	1948	1949
April	93.7	153.5	61.4	81.2	118.8
May June	230.0	199.5	127.6	150.2	87.0
June July	113.7	100.5	254.5	193.0	138.1

as previously stated, most meteorological stations record the relative humidity once a day. Leuchars, however, keeps a continuous record and this is obviously of more value for the present work than any other station records. Table IV summarizes the mean monthly values for the relative humidity at 0500, 0900, 1500, and 2100 hours in the years under review.

The interesting feature emerging from this table is that in the months of July and August, the relative humidity is consistently higher in the years 1945 and 1947 than in the remaining years (slight rust). July and August are the months when the infection would build up and spread in case of severe rust. Uredospores first appear about mid June, and by the end of June the second crop would be attacked. The climatic conditions prevailing thereafter would be of vital importance if the amount of infection was to build up to epidemic proportions.

as Scotland is concerned most meteorological stations record the relative humidity only once in the day, usually at 9 a.m. G.M.T. To be of more value, a continuous record should be kept and the instrument used should be frequently checked. Insufficient checking may have been partly responsible for the discrepancies in many published results of work dealing with relative humidities.

Freeman and Johnson(1911) could find little correlation between the relative humidity in rust years and non-rust years. Craigie refers to two German reports that severe black rust infection was linked with periods of high relative humidity.

As previously stated, most meteorological stations record the relative humidity once a day. Leuchars, however, keeps a continuous record and this is obviously of more value for the present work than any other station records. Table XVI summarizes the mean monthly values for the relative humidity at 0300, 0900, 1500, and 2100 hours in the years under review.

The interesting feature emerging from this table is that in the months of July and August, the relative humidity is consistently higher in the severe rust years (1945 and 1947) than in the remaining years (slight rust). July and August are the months when the infection would build up and spread in years of severe rust. Uredospores first appear about mid June, and by the end of June the second crop would be present. The climatic conditions prevailing thereafter would be of vital importance if the amount of infection was to build up to epidemic proportions.

As far as the other months are concerned no definite relationship can be seen, but examination of the table will show that the relative humidity of most months tends to be higher in severe rust years. It is interesting to note the unusually low moisture content of the air in 1949. This in itself is unfavourable for the development of the rust.

Table XVII gives the relative humidities for each month at Boghall and Marchmont. These are stations which record at 9 a.m. only and the results are therefore not so dependable. However, they show that there is a tendency for severe rust years to have a higher relative humidity than years of slight rust, but the relationship is not very pronounced.

(vi) The relative humidity within a crop

All these records of humidity are made in freely circulating air. The humidity of the air within a standing crop is, however, considerably higher during periods of dry weather than in the surrounding air. This was demonstrated at Boghall during July, 1949, using the method described below:-

Three hygrographs with weekly clocks were set going alongside one another for two weeks so that they could be adjusted and synchronised. Identical screens of thick white cardboard were made just big enough to cover each instrument.

The hygrographs and screens were then carefully transferred to a field of strongly growing oats and were mounted within the crop on light wooden stands placed about 100 feet from the boundary of the crop. One instrument was placed just at the level of the

the heads of the oats (4 feet above the ground), the second instrument was placed about half way up the crop and the third instrument was placed on a wooden base on the ground. The platform supporting each instrument was perforated to assist ventilation. Care was taken to distribute the instruments as little as possible.

TABLE XVII

THE RELATIVE HUMIDITY OF THE AIR FOR EACH MONTH FROM
The APRIL TO AUGUST AT TWO STATIONS

		1945	1947	1946	1948	1949
April	Marchmont	74	79	72	78	76
	Boghall	84	82	79	75	88
May	Marchmont	80	82	75	76	69
	Boghall	84	87	85	75	70
June	Marchmont	73	82	71	79	71
	Boghall	78	80	80	75	72
July	Marchmont	81	80	78	75	75
	Boghall	81	83	84	80	75
August	Marchmont	84	80	81	81	77
	Boghall	87	83	84	82	80

elsewhere. There is not so much difference between the top and middle.

Rain on the 5th broke a very dry spell and the reserve of moisture at the soil level was

the heads of the oats (4 feet above the ground), the second instrument was placed about half way up the crop and the third instrument was placed on a wooden base on the ground. The platform supporting each instrument was perforated to assist ventilation. Care was taken to disturb the crop as little as possible.

The charts were changed on the seventh day, and the instruments were interchanged so that the results would not be affected by any idiosyncracies of a particular instrument.

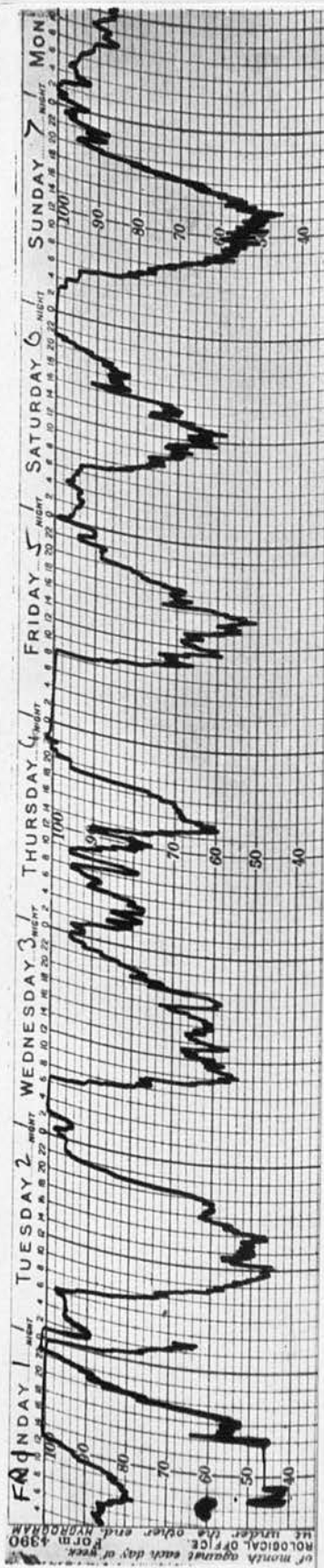
Unfortunately after the eleventh day the weather broke and became very showery so that the experiment had to be discontinued.

Fig. 12 shows the records on the three charts for a period of about seven days. It will be seen that the relative humidity at the bottom of the crop never fell below about 60% whereas the relative humidity at the level of the heads of the crop fell to about 45% at that time. Generally speaking when the relative humidity at the upper surface of the crop is at its lowest, the relative humidity at the middle is about 6 to 10% higher, and at the bottom 15 to 25% higher.

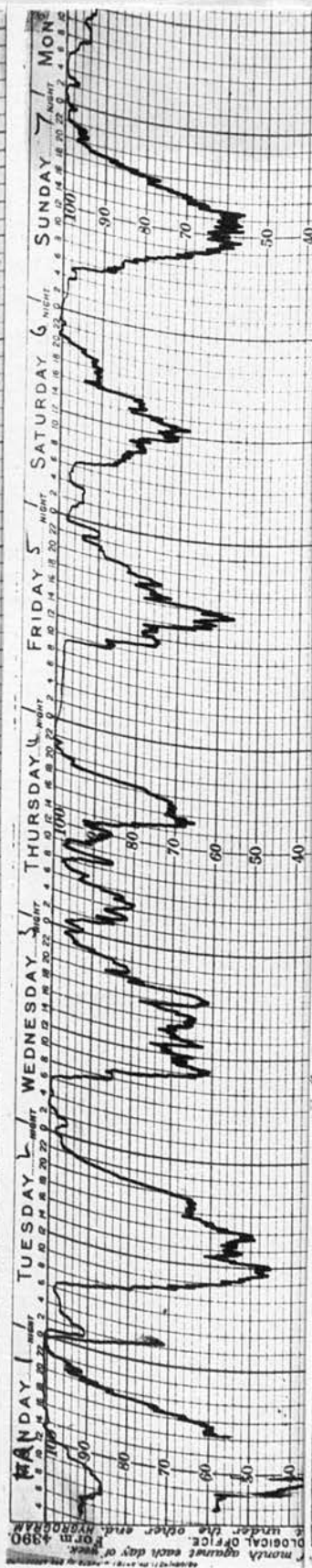
The number of hours when a 100% relative humidity existed was calculated for each day. The results are given in Table XVIII. In most days a 100% obtains for longer in the bottom of the crop than elsewhere. There is not so much difference between the top and middle.

Rain on the 5th broke a very dry spell and the reserve of moisture at the soil level would be

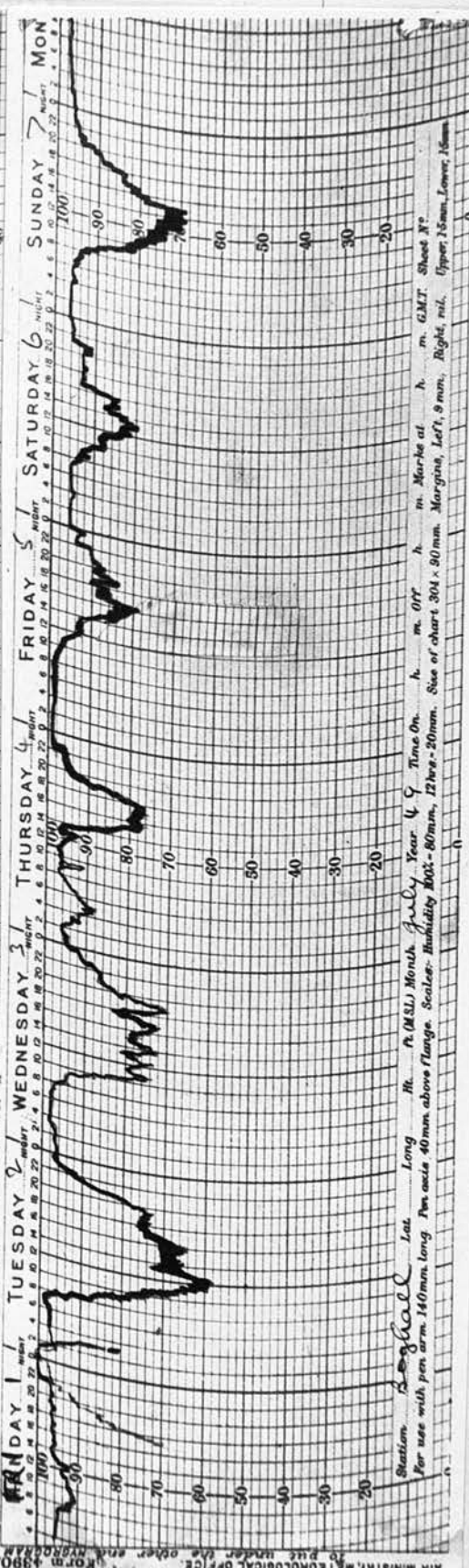
Fig. 12.



Top



Middle



Bottom

Station: Baghall Lat. Long. H. P. (MSL) Month July Year 4 Time On. h. m. Off. h. m. Mer-ke at h. m. G.M.T. Sheet No.
 For use with pen arm 140mm, long Pen scale 40mm above flange. Scales: Humidity 80%-100mm, 12hrs-50mm. See of chart 304 x 90mm. Margins, Left, 9mm, Right, nil. Upper 15mm, Lower, 15mm

Photographs of a seven day record of the relative humidity at three levels in an oat crop.

rather low. The difference in humidity is seen to be about the same at all levels in the crop. However, after the rain on the 5th, the difference became greater

TABLE XVIII
THE NUMBER OF HOURS OF 100% RELATIVE HUMIDITY AT THREE LEVELS IN AN OAT CROP

July	Top	Middle	Bottom
1-2	2½	2½	2
2-3	4	3½	4
3-4	0	0	0
4-5	10	11	11½
5-6	½	1½	6
6-7	6	4	6
7-8	1½	5	12
8-9	11	12	12
9-10	7	7	8
10-11	6	6	7
11-12	4	4	6

This short experiment indicates that within a crop, especially an oat crop, the relative humidity is always higher than it is in freely circulating air. Figures for the relative humidity obtained in Stevenson screens are obviously useful, but within a crop conditions favourable for spore germination and infection would persist longer than the screen readings would indicate.

(vii) Frequency of dew.

Everyone is well aware that heavy dews are frequently experienced in the summer months. However, they are extremely difficult to record and although the presence of dew provides ideal conditions

rather low. The difference in humidity is seen to be about the same at all levels in the crop. However, after the rain on the 5th the humidity became greater at the bottom of the crop. The cardboard screens dried out very quickly after this rain and so did not affect the readings on the chart to any extent.

Only one other suitably dry spell presented itself in 1949 and the experiment was repeated in a crop of wheat. Unfortunately some obstruction prevented the arm of the bottom instrument from rising above 80%. The results show, however, that in wheat there is very little difference if any in the relative humidity at the level of the heads of wheat, and in the centre of the crop. It was seen that the humidity at the ground level was about 10% higher than the humidity at the level of the heads of the crop, when the latter level was at its lowest, i.e. between 2 and 3 p.m.

This short experiment indicates therefore that within a crop, especially an oat crop, the relative humidity is always higher than it is in freely circulating air. Figures for the relative humidity obtained in Stevenson screens are obviously useful, but within a crop conditions favourable for spore germination and infection would persist longer than the screen readings would indicate.

(vii) Frequency of dew.

Everyone is well aware that heavy dews are frequently experienced in the summer months. However, they are extremely difficult to record and although the presence of dew provides ideal conditions

for spore germination and infection no records are available so that vague generalisation can only be made.

Craigie (1945) considers the frequent occurrence of dew to be an important factor in building up rust epidemics in West Canada. Lambert (1929) states that in parts of the Mississippi valley severe rust epidemics sometimes develop where rain was entirely absent. He suggests that heavy dews may account for this condition:

Generally speaking, on any calm clear night, dew will form. The summer of 1947 gave weeks of such night conditions and dews were noticeably heavy in the morning. The severity of the rust in 1947 has already been stressed.

3. RELATION OF TEMPERATURE TO BLACK RUST DEVELOPMENT

The temperature requirements for uredospore development and germination have received much attention from scores of workers. Mehta (1923) working at Cambridge found that spores would germinate between 35° and 86° F, with the upper limit for the optimum about 70°F. Stock (1931) gives the range for ready germination as 51° - 72° F with the optimum temperature for germ tube development about 68°F. Hwang (1942) found that the uredospores of Puccinia graminis tritici race 36 could very well withstand a temperature of 111° F for 48 hours, but at 122° F they lost viability rapidly. Scottish material of uredospores from oats left for five hours of 122° F gave 90% germination on 1% agar. However, after 24

hours at that temperature less than 1% germinated. The same material stored at 50° F for four days gave 79% germination but storing for the same period at 37° F resulted in 30% germination.

The writer has observed that when inoculating plants high temperatures such as 70° to 80° F are in no way detrimental to the subsequent infection and development of the rust. It has been repeatedly shown that for infection and subsequent development within the host, the optimum temperature is somewhat higher than for spore germination. Johnson and Newton (1937) found the best development occurred between about 65° and 74° F. As temperatures rise above the optimum the less vigorous is pustule development. They also state the interesting point that races collected in the field are more tolerant of high temperatures than artificially produced races. Peltier (1923) found the optimum temperature for the development of two forms P.graminis tritici to be 68° to 77° F. He obtained no infection at or below 50° F or above 86° F. Mehta (1923) obtained a few uredosori after 21-22 days when the average temperature was 40° F. In Scotland a similar result has been obtained with P. graminis avenae inoculations. P. graminis tritici spores inoculated at the same time did not give rise to any infection. The writer has observed that as late autumn and winter approaches the incubation period lengths from the eight to ten days of the summer to about 20 days and at the same time the numbers of sori which are produced steadily decrease.

(i) Seasonal temperatures

As already indicated, black rust is of far greater importance in some seasons than in others. From the previous paragraph it is obvious that temperature plays an important part in the initial infection and subsequent development of the rust. The temperature data from the seven meteorological stations have been examined to ascertain the extent that the variability in the amount of infection present in the various seasons may be attributed to differences in temperature conditions.

Tables XIX and XX give the average mean maximum and minimum temperatures for the six month period April to September, and the four month period May to August. During April and May the teleutospores are germinating and spermatia and aecidia appear. In June, July and August uredospores are produced which under favourable conditions spread the disease. September is included because in some seasons, the cereals are still uncut, and of course the rust is still active on wild grasses.

Examination of Tables XIX and XX will show that the six month averages for the years of severe rust are higher in every case than the corresponding averages for the slight rust years. 1949 was rather an intermediate year, the temperature averages being as high as in 1945 and 1947. However, reference to the previous section on humidity will show that there was a distinct shortage of rainfall in the early part of 1949, and this lack of moisture was unfavourable for the early development and spread of the rust.

TABLE XIX

AVERAGE MEAN MAXIMUM TEMPERATURES FOR THE MONTHS APRIL TO SEPTEMBER AT EACH STATION (°F)

Leuchars		1945	1947	1946	1948	1949	Average
Leuchars	April - Sept.	62.0	60.9	61.3	59.9	63.2	59.7
	May - August	63.5	62.8	62.4	60.9	64.8	61.8
Cupar							
Cupar	April - Sept.	62.1	62.1	61.5	61.3	63.5	60.1
	May - August	63.8	64.3	62.9	63.0	65.1	62.4
Boghall							
Boghall	April - Sept.	60.9	60.8	59.9	59.4	61.0	58.5
	May - August	62.5	63.6	61.5	61.2	62.8	60.8
N. Berwick							
N. Berwick	April - Sept.	61.3	60.4	60.8	60.2	63.4	60.5
	May - August	62.7	61.8	61.8	61.5	65.0	62.6
Marchmont							
Marchmont	April - Sept.	61.5	62.0	60.6	59.9	No record	59.6
	May - August	63.0	64.9	62.1	61.4	No record	61.8
Kelso							
Kelso	April - Sept.	62.5	62.1	60.8	60.4	63.8	61.4
	May - August	64.0	65.1	62.0	62.0	65.5	63.9
Eskdalemuir							
Eskdalemuir	April - Sept.	60.1	60.5	58.5	58.5	-	58.1
	May - August	61.9	63.8	60.0	60.4	62.8	60.5

TABLE XX

AVERAGE MEAN MINIMUM TEMPERATURES (^oF) FOR THE MONTHS
APRIL TO SEPTEMBER AT EACH STATION

		1945	1947	1946	1948	1949	Average
Leuchars	April - September	47.3	48.1	46.6	46.2	47.3	45.1
	May - August	48.7	49.8	47.7	47.5	47.9	46.9
Cupar	April - September	47.0	47.8	No Record	44.2	46.8	45.1
	May - August	48.5	49.6	No Record	44.9	47.5	47.1
Boghall	April - September	46.1	47.0	45.7	45.7	46.9	45.3
	May - August	47.5	49.2	46.5	47.1	51.0	47.1
N. Berwick	April - September	46.6	46.8	46.4	45.3	47.6	46.1
	May - August	48.0	48.6	47.3	46.6	48.3	47.8
Marchmont	April - September	45.9	46.8	45.1	45.1	46.8	44.2
	May - August	47.5	49.2	45.8	46.4	47.5	46.1
Kelso	April - September	45.9	46.2	44.7	45.9	45.9	44.6
	May - August	47.5	48.4	46.5	45.4	46.7	46.6
Eskdale-muir	April - September	43.0	44.3	41.9	42.7	-	42.0
	May - August	44.9	47.0	42.6	44.1	44.7	44.2

It can be seen that these six month averages were for most stations above the normal, even in years of slight rust development. Thus any year in which the average temperatures were below normal would almost certainly be a year of very slight rust development.

The average mean temperatures in the four month periods are also considerably higher in the severe rust years than in the other classes of year. During these months the rust may be said to be most active, and meteorological conditions then would be of vital importance in determining the scale of development of the rust.

(ii) Mean monthly temperature

The previous section has dealt with the seasonal maxima and minima. In this section the mean temperature data for May, June, July and August are considered in relation to the incidence of the rust in each year. Table XXI contains this data.

As far as May is concerned it will be seen from this table that at most stations the general mean of the average daily temperature was above average in the five years given. During the month of June, however, there was a distinct tendency for the mean temperature in 1945 and 1947 to be above that of 1946 and 1948. This is especially true of the station in the Border counties where after all the rust is found to the greatest extent. It will be seen that generally speaking the mean temperatures for each month in 1949 was as high or even higher than the same months in 1945 and 1947. However, as stressed

TABLE XXI

THE MONTHLY MEAN TEMPERATURES (°F) FROM MAY TO AUGUST AT
EACH STATION

		1945	1947	1946	1948	1949	Average
Leuchars Kelso	May	50.0	49.7	48.5	48.7	50.1	48.3
	June	55.5	55.8	55.0	53.9	54.8	53.9
	July	60.3	58.4	59.9	58.3	61.8	58.3
	August	58.7	61.3	56.8	56.1	58.8	56.9
Cupar Baskdalemuir	May	50.3	50.8	49.5	48.8	50.6	-
	June	55.8	56.0	No Record	53.7	55.8	-
	July	60.3	59.7	"	52.6	59.8	-
	August	58.2	62.1	"	55.9	59.1	-
Boghall	May	49.0	50.9	51.0	49.5	49.5	47.8
	June	54.9	55.2	52.6	54.5	55.0	53.5
	July	59.0	58.4	57.1	57.9	58.7	58.1
	August	57.0	61.0	55.3	54.7	58.1	56.5
N. Berwick	May	49.5	48.5	48.7	48.4	51.4	48.9
	June	54.9	55.3	54.0	54.0	55.3	54.6
	July	59.4	57.9	59.2	57.6	60.2	59.3
	August	57.6	59.3	56.2	56.0	59.8	58.0
Marchmont	May	49.5	51.3	48.4	48.9	50.4	48.6
	June	54.7	56.0	53.3	53.3	No Record	53.7
	July	59.8	59.0	58.4	57.9	"	57.1
	August	57.2	62.0	55.6	55.5	"	56.5

previously the general average of 1947 was very unfavourable for the development of rust, and although temperatures were very high throughout, moisture is also important.

TABLE XXI (Continued)

In July again there was a marked increase in

		1945	1947	1946	1948	1949	Average
Kelso	May	51.1	51.1	50.4	49.2	50.1	47.3
	June	55.0	55.7	54.3	53.3	55.4	52.2
	July	60.0	58.7	58.2	58.0	59.9	55.5
	August	56.9	61.4	54.2	54.4	58.9	54.5
Eskdalemuir	May	47.9	50.1	47.9	47.7	47.3	47.3
	June	52.7	54.3	49.9	52.1	54.3	52.0
	July	56.8	56.7	55.1	56.1	56.6	55.5
	August	55.7	60.7	52.5	53.1	56.9	54.5

quite severe rust - 1947. It was also a feature of 1947 that the conditions were very favourable for the development and occurrence of the rust.

At the beginning of the season it was found that the optimum conditions for the development of rust were a few degrees higher than those for severe rust and infection. Therefore for any given infection the ideal condition is for there to be a rise in temperature as the infection and incubation processes proceed. This condition was met in 1947, and widespread distribution of the disease resulted.

previously the general dryness of 1949 was very unfavourable for the development of black rust, and although temperatures were more than favourable, moisture is then apparently more important.

In July again there are generally higher means in the severe rust years, but this feature is not so clear cut as it is in June. August is the month when the mean temperatures of the slight rust years is consistently lower than during the severe rust years. The differences in mean temperature for the two types of rust season are most pronounced for this month. During the year 1947 black rust developed to its most serious proportions. Reference to the Table will show that it was during this year that the mean temperature rose each month from May to August. The mean temperature did not behave in this way in the other quite severe year - 1945. It was undoubtedly this feature of 1947 that was responsible (along with favourable moisture conditions) for the widespread occurrence of the rust.

At the beginning of the section on the temperature relationships of the rust it was stated that the optimum conditions for its incubation were a few degrees higher than those for spore germination and infection. Therefore for any given infection the ideal condition is for there to be a rise in temperature as the infection and incubation processes proceed. This condition was met with in 1947, and widespread distribution of the disease resulted.

(iii) Daily minimum temperatures

In Scotland the day temperatures are virtually always favourable for the development of black rust. It is the night and minimum temperatures which might be unfavourable for the fungus and so retard its development.

Johnston, Melchers and Miller (1938) in an account of a severe epidemic in Kansas during 1937 state that minimum temperatures appear to be more important than mean and maximum temperatures. Craigie (1945) also considers minimum temperatures below average to be important, but rather in that they retard rust development and do not actually decrease the number of infections.

The minimum temperature usually occurs in the early hours of the morning. This is the time when the stomata of wheat plants are open and the majority of infections occur (Hart 1929). However Peterson (1931) claims that a considerable amount of infection occurs in many wheat varieties even when the stomata are closed.

In order to ascertain the possible relationship of minimum temperatures to black rust development in Scotland, these temperatures were analysed in 14 day periods from 1 June to 9 August. The period 1 June to 14 June is the usual time for the first liberation of aecidiospores and subsequent infection of grasses. Thereafter the uredospores develop and spread.

Table XXII contains the mean minimum temperatures for these 14 day periods for four stations, the records for each day of which are available.

TABLE XXII

GENERAL MEANS OF THE MINIMUM TEMPERATURES ($^{\circ}\text{F}$) FOR THE
FOURTEEN DAY PERIODS 1 JUNE TO 14 JUNE, 15 JUNE TO 28 JUNE,
29 JUNE TO 12 JULY, 13 JUNE TO 26 JULY, 27 JULY TO 9 AUGUST,
AT FOUR STATIONS

Station	Period	1945	1947	1946	1948	1949
Boghall	1 June - 14 June	45.9	46.5	43.1	45.2	46.4
	15 June - 28 June	49.6	50.1	46.8	46.6	46.4
	29 June - 12 July	50.2	48.6	50.5	49.7	50.8
	13 July - 26 July	52.1	54.3	50.5	50.5	51.8
	27 July - 9 August	49.4	53.0	49.5	53.5	50.4
Leuchars	1 June - 14 June	45.9	47.7	45.3	46.8	47.3
	15 June - 28 June	50.1	50.5	48.5	48.8	46.0
	29 June - 12 July	51.0	49.6	54.2	48.7	51.5
	13 July - 26 July	52.9	53.0	53.0	51.4	51.9
	27 July - 9 August	51.3	54.3	50.7	53.4	51.9
N. Berwick	1 June - 14 June	45.6	47.1	44.7	45.0	47.3
	15 June - 28 June	49.6	49.6	47.6	48.2	46.0
	29 June - 12 July	50.3	48.4	51.1	48.7	51.2
	13 July - 26 July	52.4	53.3	52.2	48.7	51.7
	27 July - 9 August	49.8	52.5	51.0	52.9	52.7
Marchmont	1 June - 14 June	46.0	48.3	42.7	42.0	45.8
	15 June - 28 June	49.2	50.1	46.3	46.7	46.2
	29 June - 12 July	50.3	49.2	50.0	47.7	50.4
	13 July - 26 July	52.1	53.2	50.3	50.7	52.5
	27 July - 9 August	49.5	52.8	50.1	54.4	46.9

From this Table it can be seen that there is a general tendency in the years of slight rust development for mean minimum temperatures to be somewhat lower than in years of severe rust. There are two periods in which the mean minimum temperatures are at each station highest in the severe rust years, namely 15 June to 28 June and 13 July to 26 July. The first of these periods is important because as stated several times previously, the first uredospores appear during this period and the high temperatures would tend to shorten the incubation period of the rust and allow successive generations to be produced in a relatively short time, thus building up infection.

It can be also seen from the Table that in 1949 the period 1 June to 14 June had rather high minimum temperatures at each station, but as indicated when discussing moisture relationships the period was too dry to allow the fungus to develop.

Dealing further with the minimum temperatures the writer has worked out the number of days in each month when the minimum temperature was above average. The total of the number of degrees each day's minimum temperature was above average was also obtained. This was done for the months April to August inclusive, for the stations Leuchars, Marchmont and Kelso. The results are given in Table XXIII. There is a distinct tendency for years of severe rust to have a large number of days with minimum temperatures above average. Years of slight rust have almost consistently a smaller number of

TABLE XXIII

THE NUMBER OF TIMES AND NUMBER OF DEGREES THE MINIMUM TEMPERATURE WAS ABOVE AVERAGE AT THREE SELECTED STATIONS

KELSO

	1945	1947	1946	1948	1949
	Times De- grees	Times De- grees	Times De- grees	Times De- grees	Times De- grees
April	22 118	19 94	27 172	15 78	18 128
May	20 107	14 63	12 38	12 41	13 34
June	12 54	23 107	15 47	11 37	14 40
July	20 65	18 66	No Record	11 55	19 69
Aug.	7 21	17 59	No Record	No Record	20 58

LEUCHARS

April	22 118	22 103	22 115	17 89	21 144
May	22 71	24 75	19 63	17 54	17 59
June	19 65	26 90	13 49	20 46	20 55
July	22 68	21 64	21 73	19 54	21 59
Aug.	24 68	28 143	16 37	21 54	22 91

MARCHMONT

April	24 103	22 83	23 108	19 91	21 140
May	24 71	25 104	12 51	16 43	17 72
June	16 64	24 124	11 33	16 31	16 53
July	21 98	22 86	16 50	15 65	20 74
Aug.	24 53	28 105	16 34	19 62	23 88

days with above average minimum temperatures.

Considering next the accumulated number of degrees above average those for severe rust years are considerably higher than for those of slight rust years.

The year 1949 is again an exception in certain months, but as previously indicated, rainfall was the limiting factor in this year.

(iv) Temperature within a crop

As with relative humidity temperature conditions within a crop are quite different from those obtaining in the surrounding air. Roussakov (1924) found some interesting variations. The temperature registered by the screen thermometer during the daytime is generally lower by $1\frac{1}{2}^{\circ}$ to 3° F than that in the midst of the crop. The night minimum of the screen temperature is 3.6° - 7.7° higher than amongst the crop. Also within the crop the highest day temperature occurred at four inches from the soil the lowest night temperature at mid height of the plants.

During the summer of 1947 some very interesting results were obtained in Scotland (Paton, 1948) on the temperatures within a wheat field. The general method for obtaining the results was the same as that adopted for ascertaining the relative humidity at different levels in a crop (page 82). A Thermograph was placed also at a height of $3\frac{1}{2}$ feet over bare soil in the open. The observations are so interesting that a portion of Paton's table of results is given in Table XXIV.

TABLE XXIV.

DAILY VALUES OF MAXIMA MINIMA AND RANGES OF TEMPERATURE AT THREE LEVELS
IN A WHEAT CROP. (After Paton 1948).

Aug.	Min.	Max.	Range	Min.	Max.	Range	Min.	Max.	Range	Min.	Max.	Range
4	54.0	77.0	23.0	53.0	78.0	25.0	53.0	80.0	27.0	56.0	72.0	16.0
5	54.5	78.0	23.5	54.5	79.5	25.0	54.0	81.0	27.0	56.0	71.0	15.0
6	56.5	66.5	10.0	55.5	66.5	11.0	55.5	66.5	11.0	59.0	65.0	6.0
7	48.0	69.5	21.5	48.0	73.0	25.0	49.0	74.0	25.0	53.0	70.0	17.0
8	43.5	70.5	27.0	42.5	72.0	29.5	42.5	77.0	34.5	47.5	69.0	21.5
9	50.0	72.0	22.0	50.0	74.0	24.0	No record			52.0	70.5	18.5
10	50.5	68.0	17.5	51.0	69.0	18.0	50.5	72.0	21.5	55.0	68.0	13.0

Paton states that 'each day the highest temperature was recorded in the afternoon at a height of 1 foot 6 inches within the wheat. On a quiet day perceptible differences between the temperature of the air in and over the wheat and of the air over bare soil begin to appear about an hour before midday (G.M.T.) and by 1400 hours the air temperature at middle levels within the wheat may be as much as 5° F higher than the temperature at the wheat heads 2 feet above, and 7° F above the temperature at 3 feet 6 inches above bare soil in an adjacent field, conditions which may persist for several hours.' At night the results showed that when cloud was present there was rarely any noticeable difference between the temperatures within and outside the wheat. On a few misty quiet nights the temperature remained about 1° F higher within and over the wheat. Minimum temperatures were reached noticeably later at ground level in the wheat than above it.

The range of temperature at the top and middle of the crop is always considerably greater than it is in the open. The range is least at the bottom of the crop.

It was decided to repeat the experiment at Boghall in 1949 but the weather was rather unsettled and the required dry spell lasted for a comparatively few days only. The instruments were set up in wheat in the same way as Paton did in 1947, three in the crop, but the fourth or "control" was placed this time in a Stevenson screen. The results are set out in Table XXV

TABLE XXV

THE DAILY VALUES OF MAXIMA MINIMA AND RANGE OF TEMPERATURE ($^{\circ}\text{F}$) WITHIN A WHEAT CROP

July	Maxima				Minima			
	Top	Middle	Bottom	Screen	Top Range	Middle Range	Bottom Range	Screen Range
22	80°	78°	74°	71°	51° 29°	51° 27°	57° 17°	54° 17°
23	79°	78°	74°	69°	54° 25°	55° 23°	58° 16°	56° 13°
24	77°	80°	75°	70°	48° 29°	51° 29°	55° 20°	53° 17°
25	82°	82°	78°	75°	57° 25°	58° 24°	60° 18°	58° 17°
26	77°	77°	72°	70°	50° 27°	52° 25°	57° 15°	55° 15°
27	74°	75°	72°	68°	52° 22°	52° 23°	54° 18°	54° 14°
28	69	70	69	64				

The experiment was then repeated placing the instruments in a strong growing oat crop. This time ten favourable days were encountered before the onset of heavy rain.

Table XXVI gives the results for the experiment in oats.

The results this time are quite different as one might expect from the different growth habit of the two crops. The highest temperature reached with the oat crop is always at the level of the panicles. The middle height is somewhat cooler and the bottom of the straw level the coolest. Likewise the lowest temperature reached occurs at the top of the crop, the highest minimum being at the bottom of the crop. The bottom of the crop does not therefore experience the large range of temperature as does the top. During the period of the experiment the heads experienced a range of 9 to 34, the middle a range of 8 to 30 and the bottom level of the crop 5 to 25° F. The screen temperature range was very similar to that at the lower level.

Thus the oat panicles form a barrier to the sun's rays and the interior of the crop is not warmed at the same extent as the wheat crop.

The considerable amount of infection which occurs on the oat panicle may therefore be partly accounted for by the comparatively high temperatures which occur in that region.

4. RELATION OF LIGHT TO BLACK RUST DEVELOPMENT

The black rust fungus cannot be grown apart from its hosts, which are chlorophyll bearing plants.

TABLE XXVI

THE DAILY VALUES OF MAXIMA MINIMA AND RANGE OF TEMPERATURE ($^{\circ}\text{F}$) WITHIN AN OAT CROP

July	Maxima				Minima			
	Top	Middle	Bottom	Screen	Top Range	Middle Range	Bottom Range	Screen Range
2	77°	75°	71°	71°	49° 28	50° 25	52° 19	51° 20
3	76°	74°	71°	70°	49° 27	50° 24	52° 19	50° 20
4	73°	69°	67°	66°	53° 20	55° 14	55° 12	58° 8
5	65°	60°	57°	61°	48° 17	48° 12	49° 8	50° 11
6	65°	63°	61°	60°	47° 18	48° 15	49° 12	50° 10
7	74°	70°	66°	67°	43° 31	45° 25	47° 19	46° 21
8	63°	62°	60°	60°	54° 9	54° 8	55° 5	55° 5
9	76°	74°	71°	71°	42° 34	44° 30	46° 25	47° 24
10	79°	75°	73°	73°	46° 33	47° 28	50° 23	49° 24

Light is vital for the growth of these plants and thus at least indirectly, light is indispensable for the fungus. The stomata also open in the light and may facilitate the entrance through them of the germ tubes.

There are, in the literature, diverse opinions as to whether or not the rust spores will germinate at night. Craigie (1945) put spores in extreme darkness and obtained 30 to 40% spore germination in less than three hours. Bruschetti (1933) found that light and darkness had no effect on uredospore germination. Stock (1931) states that the development of Puccinia graminis was distinctly checked by light, while the uredospores of P. triticea, P. secalina and P. lolii germinated equally well in light or in darkness. Uredospores from Scottish material germinate well in complete darkness. Sibia (1928) could not germinate spores in darkness.

Bright sunlight, however, directly effects the capacity of the spores to germinate. Dillon Weston (1931) working at Winnipeg obtained no germination of uredospores exposed to sunlight or very strong diffused light, whereas a similar set of spores kept in the dark germinated readily. Results in Minnesota (Hwang 1942) have shown that the effect of sunlight is temporary only and not detrimental. Once suitable conditions appeared again (moisture etc.) spores germinated and a high incidence of infection was secured.

How far the entry of the fungus into the host is affected by light is not altogether clear.

Peltier (1925) came to the conclusion that light has no influence whatever on infection of wheat seedlings by black rust uredospores. Darkness at the time of inoculation and throughout the early stages of infection was found by Hart and Forbes (1935) to diminish the prevalence and intensity of the symptoms produced by the wheat black rust. Although no critical experiments were made by the writer on this point, during the summer months it seemed to make no difference to the amount and type of infection produced whether the plants were inoculated at dusk or in the forenoon. The incubation chambers were, however, placed so that direct sunlight never fell on them.

Once the plants have become infected there is general agreement that bright light induces most vigorous and rapid growth of the fungus in the host tissues.

(1) Sunshine hours in S. E. Scotland

The monthly totals of hours of sunshine from April to September for four stations are given in Tables XXVII-XXX. Examination of the tables will show that there is little if any correlation between the number of hours of sunshine in each month, and the type of rust year. The month of May has consistently fewer hours of sunshine in the severe rust years than in the years of slight rust. The only month which in the five years under review has a greater number of sunshine hours in both severe rust years than in any of the other years is August. The amount of sunshine in April, June, July and September

TABLE XXVII.

THE NUMBER OF HOURS OF SUNSHINE IN EACH MONTH FROM
APRIL TO SEPTEMBER.

Leuchars.

	<u>1945</u>	<u>1947</u>	<u>1946</u>	<u>1948</u>	<u>1949</u>	<u>Av.</u>
April	179.2	145.8	187.2	193.4	186.0	149
May	183.6	161.5	243.8	219.4	232.9	177
June	213.1	136.2	217.7	168.1	263.6	203
July	187.3	192.6	177.5	189.2	205.2	172
Aug.	166.8	213.6	163.3	104.1	159.2	155
Sept.	113.4	137.5	121.4	155.4	152.2	139

TABLE XXVIII

THE NUMBER OF HOURS OF SUNSHINE IN EACH MONTH FROM
APRIL TO SEPTEMBER.

Boghall.

	<u>1945</u>	<u>1947</u>	<u>1946</u>	<u>1948</u>	<u>1949</u>	<u>Av.</u>
April	179.9	122.7	156.6	137.4	138.7	124
May	165.5	133.9	203.9	212.2	194.7	157
June	173.6	132.5	152.5	135.4	241.8	193
July	159.6	152.2	134.0	138.5	176.5	167
Aug.	154.3	238.2	128.6	90.7	124.5	143
Sept.	102.4	113.4	77.9	129.4	111.8	128

TABLE XXIX.

THE NUMBER OF HOURS OF SUNSHINE IN EACH MONTH FROM
APRIL TO SEPTEMBER.

MARCHMONT.

	1945	1947	1946	1948	1949	Av.
April	170.0	115.6	161.8	146.7	130.3	136
May	151.9	126.1	196.3	195.3	212.4	165
June	168.8	107.6	157.7	147.0	234.8	190
July	165.5	154.8	137.7	135.7	181.7	164
Aug.	138.8	223.2	127.2	91.9	141.5	143
Sept.	104.4	99.8	69.5	118.3	115.5	126

TABLE XXX.

THE NUMBER OF HOURS OF SUNSHINE IN EACH MONTH FROM
APRIL TO SEPTEMBER.

ESKDALEMUIR.

	1945	1947	1946	1948	1949	Av.
April	169.1	80.2	149.3	123.5	116.4	127
May	133.8	149.6	254.2	230.8	204.8	161
June	144.4	104.9	136.0	131.1	232.2	175
July	142.5	117.0	128.2	160.1	172.5	148
Aug.	181.0	259.7	101.7	70.0	138.8	121
Sept.	72.5	94.8	54.9	83.1	--	111

appears to have no relationship whatsoever to the type of rust year. The total number of hours of sunshine, therefore, apparently bears little relationship to the type of rust year.

Craigie (1945) came to the same conclusion as far as the rust in Western Canada is concerned. It is interesting to note that he also found that August was the only month when there was a tendency for severe rust years to have a somewhat greater number of hours of sunshine than the slight rust years.

5. RELATION OF WIND TO BLACK RUST DEVELOPMENT

In parts of America and Canada where the barberry has been eradicated the only source of infection is by means of air borne uredospores. Craigie (1945) in Western Canada has carried out a detailed examination upon the frequency of various winds in relation to stem rust outbreaks. The south wind appears to be the all important one which carries with it the bulk of the inoculum. In Manitoba particularly, there was a close association between the occurrence of a south wind and that of severe rust attacks.

In S. E. Scotland, on the other hand, the barberry is quite plentiful, providing the source of inoculum each season, and the wind direction is of no importance as far as initiating an attack. From an agricultural point of view of course, wind direction is important in that susceptible crops growing on the leeward side of barberries will become more severely attacked than those on the windward.

The records from the seven stations of the wind

directions in each year gave no correlation between the amount of rust in any year and the number of times the wind came from a certain quarter.

6. CONCLUSIONS

The foregoing account indicates that for black rust to develop to serious proportions, the following meteorological conditions are necessary during the active period of the rust i.e. April to September.

Temperatures during the months April to June to be above average with plentiful and frequent rainfall.

The months of July, August and September to be warm or very warm with only moderate amounts of rainfall. Clear skies at night following warm sunny days are conducive to dew formation, such conditions being ideal for uredospore germination and infection.

extend with the rust. The effect of climatic conditions on the development of the rust is discussed in the spring.

The writer has, however, examined the climatic conditions from 1914 to 1924 and the development of the rust from 1914 to 1924. The results are briefly reported in the account.

It will be remembered that in the section the meteorological conditions at stations were examined. In the present account, however, three stations only are considered, all the stations being examined at the same time. The stations considered are those at Haskelton, Haskelton, Haskelton.

The meteorological conditions at Haskelton.

PART XIII

THE RELATION OF THE METEOROLOGICAL CONDITIONS
OF THE PREVIOUS WINTER TO THE INCIDENCE OF
BLACK RUST IN EACH SEASON

1. INTRODUCTION

The previous section dealt with the effect of climatic conditions on the incidence of black rust from April to September i.e. during the active period in the life cycle of the rust.

The question arises as to what effect, if any, the climatic conditions of the previous winter may have on the development of rust in any season. Very little work has been published on this aspect, and most of that which has deals with the effect of winter conditions in relation to the survival of uredospores. Lambert (1929) has dealt to some extent with the problem, but has stressed mainly the effect of climatic conditions on the germination of teleutospores in the spring.

The writer has, however, examined the winter climatic conditions from 1944 to 1948 in relation to the development of the disease from 1945 to 1949. The results are briefly reported in the following account.

It will be remembered that in the previous section the meteorological records from seven stations were examined. In the present section, however, three stations only will be considered, all the stations being south of the Forth. The stations considered are north Berwick, Kelso and Eskdalemuir.

The meteorological conditions of the months

November to March are considered, under the headings humidity and temperature.

2. HUMIDITY RELATIONSHIPS

(i) Amount and frequency of rainfall

For the three stations the total amount of rainfall from November to March and the number of days on which it fell are given in Table XXXI. The Table indicates that there is a distinct tendency for years of severe rust to be preceded by winters with considerable rainfall. The winter of 1947-48 is rather an exception, in that 1948 being a year with slight rust it was preceded by a very wet winter.

There is almost consistently a greater number of days with a measurable rainfall in winters preceding severe rust years compared with the number of rain days in winters preceding slight rust years.

The Eskdalemuir stations records the actual number of hours when rain fell. The records are summarised in Table XXXII which shows very clearly that in the years under review the rainfall was much more prolonged in winters preceding severe rust years.

(ii) Relative humidity of the air

The average relative humidity of the air for the months of November to March inclusive are given in Table XXXIII. It can be seen that there is a tendency for the relative humidity to be higher in winters preceding years of severe rust.

3. TEMPERATURE RELATIONSHIPS

The average maximum and minimum temperatures for each month for the three stations are given in Tables XXXIV, XXXV, and XXXVI.

TABLE XXXI.

THE AMOUNT OF RAIN AND NUMBER OF DAYS WITH .01 INCH OR
MORE RAIN DURING THE PERIOD NOVEMBER TO MARCH.

Kelso.

	<u>1945</u>	<u>1947</u>	<u>1946</u>	<u>1948</u>	<u>1949</u>
Rain Nov.- March	13.64	14.10	6.1	13.17	7.64ins.
No. days	94	106	71	79	57

North Berwick.

Rain Nov.- March	12.66	13.23	7.57	11.55	6.59
No. days	85	92	68	85	58

Eskdalemuir.

Rain Nov.- March	37.52	30.77	20.98	22.02	29.14
No. days	117	109	93	96	94

TABLE XXXII.

THE HOURS OF RAINFALL FROM NOVEMBER TO MARCH AT
ESKDALEMUIR.

	<u>1945</u>	<u>1947</u>	<u>1946</u>	<u>1948</u>	<u>1949</u>
	739.1	727.7	456.0	589.7	535.1hrs.

TABLE XXXIII.

THE AVERAGE MAXIMUM AND MINIMUM TEMPERATURES FOR
EACH MONTH FROM NOVEMBER TO MARCH.

NORTH BERWICK.

	1944-5	1946-7	1945-6	1947-8	1948-9
Nov	46.1	35.4	50.4	40.2	50.8
Dec	43.9	34.1	48.1	38.1	48.1
Jan	38.0	28.3	40.0	32.0	40.0
Feb	48.9	36.8	44.4	33.4	44.2
Mar	52.5	38.5	47.6	34.5	47.3
Mean Av.	43.8	32.8	44.1	33.5	44.2
Nov-Mar.	39.2	34.8	40.1	39.5	40.2

TABLE XXXIII.

THE AVERAGE RELATIVE HUMIDITY OF THE AIR DURING THE
MONTHS NOVEMBER TO MARCH. (%)

	1944-5	1946-7	1945-6	1947-8	1948-9
Eskdalemuir.	87	86	87	85	87
N.Berwick.	83	83	82	80	77
Kelso.	86	86	84	88	85

TABLE XXXIV.

THE AVERAGE MAXIMUM AND MINIMUM TEMPERATURES FOR
EACH MONTH FROM NOVEMBER TO MARCH. (°F)

KELSO.

	1944-5		1946-7		1945-6		1947-8		1948-9		Av.	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Nov	44.6	33.8	48.6	37.7	48.0	40.0	48.1	33.9	50.1	35.6	46.9	34.7
Dec	42.6	33.7	41.1	29.9	43.9	34.4	42.7	32.8	45.4	33.3	43.6	33.2
Jan	36.4	24.9	39.4	30.0	40.6	30.7	40.6	32.0	46.0	32.5	43.1	32.5
Feb	48.9	36.8	34.4	22.7	46.0	35.7	44.2	33.4	47.4	33.4	44.2	32.3
Mar	52.5	38.5	39.4	25.4	47.6	34.3	52.8	34.5	47.3	31.5	47.6	33.4
Mean Av.												
Nov-Mar.	39.2		34.8		40.1		39.5		40.2			

Mean Av.
Nov-Mar. 37.3

For each station the lowest mean temperatures
for each month were in TABLE XXXV.

1945-7 THE AVERAGE MAXIMUM AND MINIMUM TEMPERATURES FOR
EACH MONTH FROM NOVEMBER TO MARCH. (°F)

NORTH BERWICK.

	1944-5		1946-7		1945-6		1947-8		1948-9		Av.	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Nov	46.1	35.4	50.4	40.2	50.2	41.0	49.7	38.1	51.9	38.9	47.4	37.2
Dec	43.9	34.8	43.0	32.8	46.1	36.4	45.7	36.2	47.5	36.8	44.2	35.7
Jan	38.0	28.3	--	33.0	43.1	31.3	42.6	34.0	48.1	35.1	44.5	34.8
Feb	48.3	37.5	--	26.9	46.3	35.8	50.1	34.9	47.8	35.7	44.1	34.7
Mar	53.4	39.4	--	28.4	47.6	35.7	52.5	37.3	48.3	34.4	47.6	35.7
Mean Av.	the conditions prevailing towards the end of the											
Nov.Mar.	40.5		--		41.3		42.1		42.4			

would be of most importance, regulating as they do
the time of opening of the barberry buds. As far as
the teleutospores of the rust are concerned they have
germinated in March each year, no matter what the

TABLE XXXVI.

THE AVERAGE MAXIMUM AND MINIMUM TEMPERATURES FOR
EACH MONTH FROM NOVEMBER TO MARCH. (°F)

ESKDALEMUIR.

	1944-5		1946-7		1945-6		1947-8		1948-9		Av.	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Nov	43.5	33.2	46.9	37.9	47.8	37.4	45.7	33.6	47.4	35.3	44.2	33.3
Dec	40.6	32.3	39.6	29.1	43.2	31.6	42.6	33.7	43.2	32.3	41.4	32.4
Jan	35.5	24.2	38.0	29.4	39.2	26.9	39.0	32.1	43.0	32.6	40.8	31.4
Feb	45.1	35.1	31.3	22.6	44.2	31.6	42.3	31.5	44.0	32.6	41.3	30.9
Mar	49.6	34.3	36.9	27.5	45.1	30.5	52.2	33.9	45.9	30.8	44.3	31.0
Mean Av.												
Nov.Mar.	37.3		33.9		37.7		38.6		38.7			

For each station the lowest mean temperatures for each month were in the winters of 1944-5, and 1946-7 i.e. the winters preceding severe rust years.

4. CONCLUSIONS AND DISCUSSION

Thus greater and more frequent rainfall, higher relative humidities, and lower temperatures tend to occur in the winter months (here taken to be November to March inclusive) preceding seasons of severe rust attack.

These observations are interesting but with the present state of our knowledge it is not easy to envisage their complete significance. It would seem that the conditions prevailing towards the end of the winter i.e. in the months of February and March, would be of most importance, regulating as they do the time of opening of the barberry buds. As far as the teleutospores of the rust are concerned they have germinated in March each year, no matter what the previous conditions have been.

PART XIV

THE RELATIONSHIP BETWEEN METEOROLOGICAL
CONDITIONS AND DEVELOPMENT OF BLACK RUST IN
THE THREE YEARS WHEN DETAILED OBSERVATIONS
WERE MADE (1947-9)

1. 1947

In 1947 the barberry buds did not begin to unfold until mid April. This was about a month later than usual, and the spermagonia were correspondingly later in appearing. The very low average mean temperature existing during the months at the end of winter and April undoubtedly accounted for this. The mean temperature for April 1947 was about 32° F as opposed to the average of 40° F. However, from May onwards the temperatures rose rapidly, rainfall was sufficient and aecidiospores appeared mid May with uredospores about three weeks later. The temperature rose each month during the summer and the disease developed and spread. The actual summer rainfall was not high, but with the clear night skies which were common in the summer of 1947 heavy dew formation resulted, creating ideal conditions for spore germination.

2. 1948

February and March (March particularly) were mild months and the barberry buds began to unfold at the more usual time of mid March. Aecidiospores appeared during the middle of the following month, but uredospores did not appear until about six weeks later, as opposed to three weeks later in 1947. Reference to the prevailing meteorological conditions will show that the average mean temperatures for May and June

were rather low, and so undoubtedly slowing up the development of the rust. The summer temperatures remained low and the rust did not develop to any extent.

3. 1949

The year 1949 was rather an interesting one forming as it did an intermediate year as far as rust development is concerned.

The previous winter was very mild, the average mean temperature being higher than in any other winter during the years under review. The spring and summer temperatures were also high, higher even than in 1947, and yet during the main part of the season there was little rust present; at least it did not spread far from the barberries. The reason for the slow development of the rust is the lack of moisture which was experienced. The November to March rainfall was low (even as recorded at Eskdalemuir - a wet station). This was followed by low rainfall in April, May and June. Conditions were therefore, far from satisfactory for rust development.

However, later in the season the rainfall increased and with the high temperatures prevailing, conditions were favourable for the rust and inoculum was built up and spread. However, in most places this was after the crops had been harvest^{ed}, and little damage was done except to those crops adjacent to barberry hedges.

SECTION 2.

PUCCINIA GLUMARUM

INTRODUCTION

In his Presidential address to the Association of Applied Biologists Mr W. C. Moore gives yellow rust as one of the forty or so most important economic diseases in Great Britain (Moore 1949). In the past yellow rust has received comparatively little attention in this country, but its importance is becoming increasingly appreciated. During recent years the disease has received considerable attention, particularly at Cambridge.

Biffen and Engledow (1926) were of the opinion that yellow rust was the most important rust of wheat. Dennis (1944) rather minimises the position of the rust in Scotland. He states that it can usually be found if hunted for. The writer, however, has seen it each year since 1945 without having to resort to any particular search.

PART IIHOST RANGE

Wilson (1934) records the uredospore and teleutospore stages of Puccinia glumarum on Hordeum vulgare, Triticum vulgare, Agropyrum repens, Elymus arenarius and Hordeum murinum. In addition to finding it on these hosts the writer has seen the rust on Dactylis glomerata.

The rust was particularly severe on this latter host in many places in the Lothians in 1949. The rust was not noticed on the grass until August. It had probably been missed previously. Sampson (1924) reports that this rust can be epidemic on cocksfoot at Aberystwyth.

PART III

THE DEVELOPMENT OF THE DISEASE EACH SEASON

The writer started making observations on cereal rusts in Scotland in 1945. However, records at the Edinburgh College of Agriculture and elsewhere show that the disease was particularly severe in 1943. Therefore in this and the section on the relationship between climatic conditions and the rust, the years 1943 to 1949 inclusive are considered.

1. 1943

Dennis (1944) remarks that as in England yellow rust was 'alarmingly conspicuous' in Scotland in 1943. Dillon Weston (1944) and Moore (1948) draw attention to the severity of the disease in England, the latter author reporting also that by April the rust had appeared earlier and more extensively in the north than in any previous season recorded.

Unpublished records of the Edinburgh College of Agriculture show that many wheat crops in the area were severely affected, particularly in East Lothian and Berwickshire.

2. 1944

The rust was present to some extent but in no way serious.

3. 1945

Only occasional slight infections were seen.

4. 1946

The rust was present on many wheat crops in the first week of April which is quite early in the season for the rust to be seen. The rust cleared somewhat towards the end of May and in June and July, but

appeared to develop again during August.

5. 1947

Very little yellow rust was seen. The rust in any case appeared late (end of June) and its place was very soon taken by Puccinia triticina. Yellow rust in 1947 seemed to be more frequent on barley than on wheat.

6. 1948

The rust appeared about the middle of May. On 12 May the rust was looked for on crops in E. Lothian but none was seen. However, ten days later pustules were appearing. By the end of June the rust was fairly severe on many wheat crops. The rust therefore developed rather quickly once it appeared.

7. 1949

The rust was found unusually early - 25 March - on a crop of Holdfast wheat at North Berwick (E. Lothian). The plants were about three inches high with, on the average, three tillers per plant. The first leaf of most tillers was severely attacked. The distal portions of these leaves were covered with uredosori. Spore production was so profuse that the soil beneath many plants was coloured yellow by the spores. The rust then appeared to spread in a south westerly direction across the Lothians. By the end of May infection was frequent in the Haddington area, and it began to appear near Dalkeith in mid June.

When visiting Crail, which is a town on the easternmost part of Fife, on 25 April a crop of wheat was found to be infected in the same way as the crop

in E. Lothian found a month previously. Many leaves were killed by the rust. It is probable therefore, that the disease was present on this crop also in March.

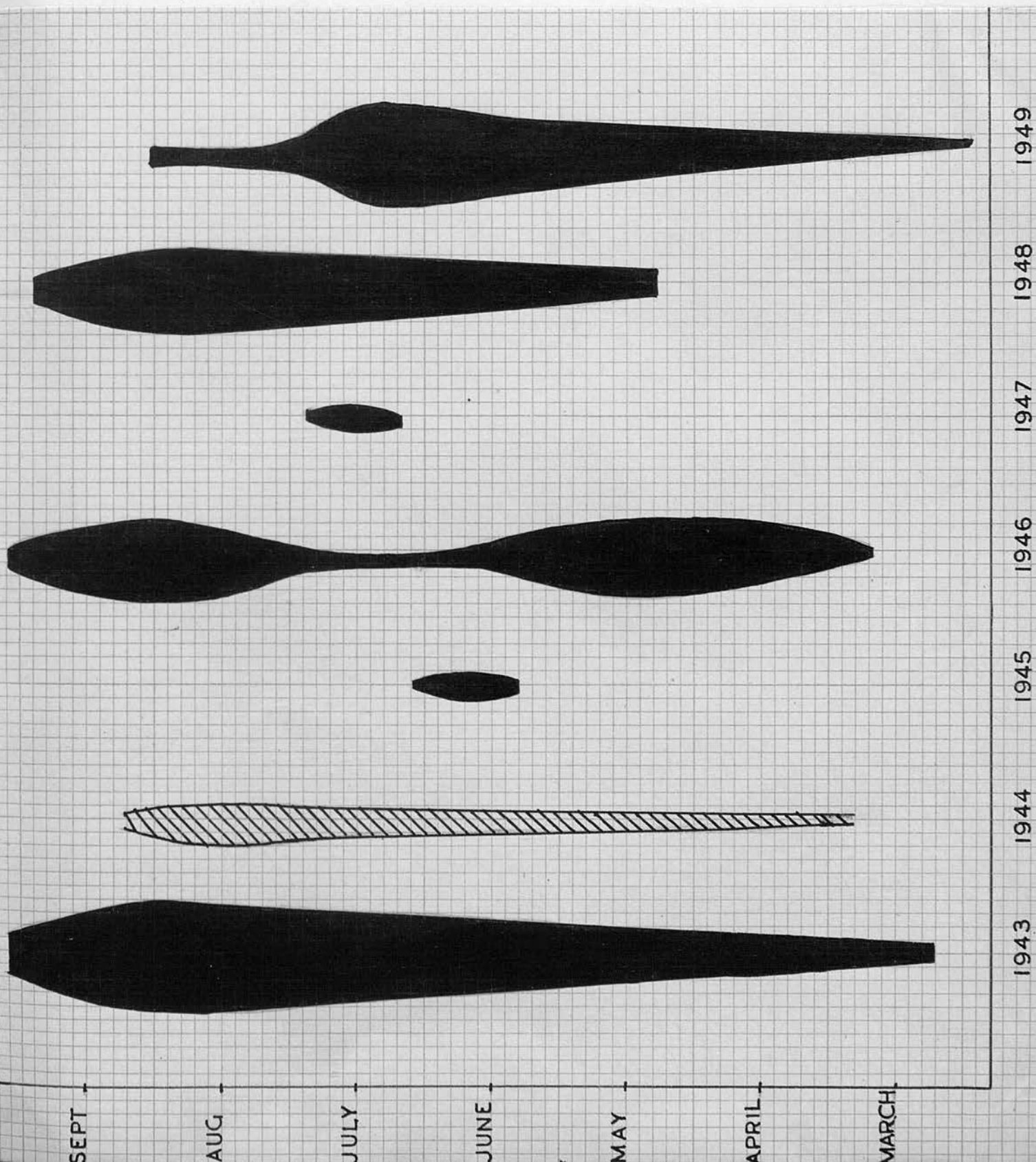
Yellow rust became quite severe on many crops throughout the College area, but the warm dry weather arrested the development and spread of the disease. By the middle of July fresh uredosori of the rust were difficult to find. By this time many of the lower leaves of susceptible varieties of wheat had been killed by the rust. On the upper leaves were white streaks and patches which marked the position of the uredosori a week or so before. It was interesting to observe how the rust had been checked in this way by the prevailing high temperatures. Because of this check, very few uredosori appeared on the heads of the wheat.

Thereafter odd uredosori and teleutosori were seen on volunteer plants until December when the writer left Edinburgh. If searched for the rust could undoubtedly have been found in January and even in February in view of the very mild winter experienced.

A diagrammatic representation of the progress of the disease in each season is given in Fig.13. The months March to September only are given in this diagram. This is the important period as far as the growth of the wheat crops is concerned.

Fig. 13.

Diagrammatic
representation
of the progress
of yellow rust
in each season.



PART IV

THE SUSCEPTIBILITY OF VARIETIES OF WHEAT AND
BARLEY TO YELLOW RUST IN THE FIELD

1. INTRODUCTION

Dillon Weston (1944) has given a list of commonly grown wheat varieties and their relative susceptibility to yellow rust in England. No such list has appeared for Scotland. The writer has therefore made observations in the field in order to obtain some information on the relative susceptibility to yellow rust of the various varieties of wheat and barley grown in S. E. Scotland.

2. OBSERVATIONS AT BOGHALL

Each year at the College Farm, Boghall, mid Lothian, a considerable number of varieties of wheat and barley are grown in plots alongside one another so that their performances can be judged and compared one with another. These plots have been examined for the occurrence of yellow rust and notes were made on each variety.

In assessing the amount of rust present, a key made up by Dr Grainger of the West of Scotland College of Agriculture was used. This is similar to the one he published for assessing mildew (Grainger 1947) and similar also to the key devised by Dr Manners at Cambridge.

The results of each year's observations are given in a summarised form in Appendix 2.

The wheat results are given first, followed by the barley results.

3. WHEAT VARIETY TRIALS IN THE COUNTIES

In the autumn of 1948 it was decided to lay

down quarter acre plots of various commonly grown wheat varieties on several farms in S. E. Scotland. Among other things it was thought that these trials would provide some information on the relative susceptibility of the different varieties to yellow rust.

Some of these trials were visited at frequent intervals. Others more distant were unfortunately only examined once.

The counties in which the trials were held, the varieties sown, and details of infection on the different dates of observation are given below.

Centre 1: East Lothian

Centre 3: Seed sown 20/12/48 at 5 bushels per acre.

Variety	Date of Observation		
	25/5	16/6	15/7
King II	0.5	1	20
Als	3	3	5
Bersee	0	0	0.5
Pilot	0.5	3	20
Scottish Iron III	1	3	1
Eroica	1	1	5

The figures refer to percentage infection.

Centre 2: Mid Lothian

Seed sown 2/12/48 at 4 bushels per acre.

Variety	Date of Observation			
	16/6	12/7	29/7	11/8
Yeoman	0	0.5	0.5	a
Pilot	0	15	40	40
Bersee	0	0	0	a
Eroica	0	2	10	15
Scottish Iron III	0	1	10	20
Als	0	0.5	1	a
Scandia	0	0.5	1	a

a = crop ripe, leaves withered.

Centre 3: Mid Lothian

Seed sown 3/11/48 at 4 bushels per acre.

Variety	Date of Observation	
	29/7	11/8
Defiant	0	0.5
Bersee	0	0
Eroica	0.5	1
Victor	1	15
Als	1	a
Pilot	1	a
King II	5	a

a = crop ripe, leaves withered.

Centre 4: Roxburghshire

Seed sown 2/12/48 at 5 bushels per acre.

Variety	Date of Observation	
	30/6	19/7
N Defiant	0	0.5
Eroica	0	0.5
Als	5 (in patches)	5
Squarehead Master	0	0
Bersee	0	0
King II	5 (in patches)	10

4. GENERAL CONCLUSIONS

The trials just referred to together with the writer's observations at Boghall and East Craigs have provided quite a lot of information on the relative susceptibilities of dozens of varieties of wheat and barley. There are, however, limitations to the value of such records. No information has been obtained on the reaction of each variety to the physiologic races of Puccinia glumarum present. Before a variety can be recommended for a particular area its reaction to the rust races present in that area must be known. Better still of course, the reaction of a particular variety to all the rust races known to exist in this country should be ascertained.

Dr Manners working at Cambridge was the first person in this country to obtain any information on the reaction of wheat and barley varieties to specific races of yellow rust. Manners found eight races of

wheat yellow rust in Britain and tested a number of wheat varieties with each race. The Cambridge Plant Breeding Institute took over the races on the completion of Manners' work and have tested other varieties.

The writer, now mycologist at the National Institute of Agricultural Botany, Cambridge, is receiving cultures of the races of yellow rust identified in this country and part of his work is to test the reaction of these races on the different wheat and barley varieties commonly grown as well as to test the new cereal varieties as they come to the Institute for trial. Samples of yellow rust from different parts of the country will also at intervals be inoculated on the differential hosts and a lookout kept for any new races which may appear. During the next few years, therefore, information should become available on the reaction of wheat and barley varieties (in the seedling and mature plant stages) to the races of yellow rust present in this country.

However, returning to the main theme of this section, from the records available, general observations can be made on the most susceptible and also most resistant varieties to yellow rust in S. E. Scotland. Dillon Weston (1944) quoting from information obtained from Dr H. Hunter of the National Institute of Agricultural Botany gives the following list of wheat varieties in order of susceptibility to yellow rust:- Desprez 80, Wilma, (Squarehead Master, Wilhelmina, Victor), Als, Scandia, (Bersee, Juliana), Jubilegem, (Steadfast, Holdfast, Yeoman), Little Joss, Rivet. The varieties listed

together in any one set of brackets are equal or very similar to one another in their resistance to yellow rust.

It is not easy to compile a list for S. E. Scotland from the material available as the observations have not been consistent each season. However, from an examination of the records, a list of the commonly grown varieties compiled in the same way as the one given in the previous paragraph is:-

(Pilot, Victor, Wilhelmina, King II), (Scottish Iron III, Eroica, Jubilegem, Als, Yeoman), (Holdfast, Squareheads Master), (Diamond II, Juliana, Scandia II), (Bersee, Vilmorin 27, Steadfast, Atle, Little Joss).

Broadly speaking the two lists are similar. Bersee, however, is a variety which in Scotland is apparently highly resistant to the rust, while in Dr Hunter's list it is at least fairly susceptible. The writer has been privileged to see Manners' results, as yet unpublished, and an explanation for the difference in position of Bersee in the two lists is supplied. In Great Britain races 2 and 3 of the rust are apparently confined to the varieties Bersee, Desprez 80, and Vilmorin 27. These two races are restricted geographically to central and southern England. Reference to the Scottish list will show that Vilmorin 27 is also in the highly resistant group. Thus unless races 2 and 3 spread northward, Bersee and Vilmorin 27 can be definitely recommended for growing in S. E. Scotland, at least as far as their susceptibility to yellow rust is concerned.

PART V

EXPERIMENTS ON THE EFFECT OF YELLOW RUST ON YIELD

1. INTRODUCTION

Yellow rust is undoubtedly the most important rust of wheat at least in this country and severe infection occurs in many seasons. Very few figures are available, however, for the actual losses caused by the rust. Dennis (1944) gives a few figures for a severely attacked crop of wheat grown in the Tweed Valley in 1943. This crop which normally would have been expected to yield about 32 bushels per acre actually threshed only 6 bushels per acre. On the average, the rust brought about a reduction in yield of about eight bushels per acre in that season.

That the rust can bring about serious loss in seed crops of cocksfoot is indicated in a report from Aberystwyth (Sampson 1924). In a rust infected cocksfoot crop grown for seed the average weight of seed from twelve panicles was 1.6 grammes with 64 per cent heavy seed. Plants grown under the same conditions but practically free from the rust yielded, on the average, 5.3 grammes of seed per twelve panicles, 83 per cent of which was heavy.

2. MATERIALS AND METHODS

(1) E. Lothian experiment

The writer thought it would be interesting to obtain, if possible, figures for the losses actually incurred by an attack of yellow rust. To this end, six plots each six yards by twenty yards were marked out in a crop of Als wheat in E. Lothian. Yellow rust

was present in this crop at the time of marking out the plots (the beginning of June) and was, from early observations, apparently increasing.

Work at the Dominion Rust Research Laboratory, Winnipeg, and elsewhere has shown that good control of rust can be obtained by dusting a crop with sulphur (Bailey & Greaney 1928).

Thus plots 1, 3, and 5, were dusted with 'Sulphocloud' (a proprietary compound, 90% of which is said to pass through a 300 mesh sieve). Thirty pounds of the dust were applied to each plot at each dusting. This quantity has been shown to give the best results in Canada. The sulphur was at the first dressing applied with a blower dust gun of the type used and pictured by Bailey and Greaney (loc. cit). It was observed, however, that the actual spread of dust into the crop was not very satisfactory when using the blower. Subsequent dressings were therefore applied by hand. In this way the dust could be applied lower in the crop and a more satisfactory cover of sulphur resulted. When dusting care was taken to walk between the rows to avoid damaging the crop.

Ideally the sulphur should be applied every week or ten days, depending partly on the weather. Heavy rain for instance would wash the dust off the crop and a further application would be necessary to control the rust. The plots were first dusted on 9 June, then on 16 June when the ears were beginning to shoot. When the crop was again visited ten days later, most of the plots were found to be badly laid.

This was very unfortunate because it was now impossible to walk in the plots without the risk of doing more damage than would have been caused by the rust even were it severe. The experiment in E. Lothian had to be abandoned.

(ii) Boghall experiment

A similar experiment was conducted at Boghall in a commercial crop of Pilot wheat. Plots ten yards by twelve yards were marked out and thirty pounds of sulphur dust applied to plots 1, 3 and 5. The dressings were always applied by hand.

The first dressing was given on 24 June. The ears had shot by the following dressing 1 July. The weather was unsettled during July and the early part of August with intermittent rain. Dressings of sulphur were therefore applied when conditions permitted, i.e. on 5, 12, 19 and 22 July and on 15 August.

The onset of very warm weather during July arrested the development and spread of the rust and very few pustules were present on the ears of the wheat. The possible beneficial effect of the sulphur dustings in helping to keep the ears free from the rust was therefore rendered negative. Also the warm yet unsettled weather brought about unsuitable conditions for controlling leaf infection. Little or no difference in the amount of leaf infection in the dusted or control plots could be detected.

To complete the experiment 200 heads were picked at random from each plot on 26 August when the crop was ready for cutting. The heads were hung in a dry

place for fourteen days and the grain was then removed by hand.

3. RESULTS

The total weight of grain from each plot and the 1000 grain weight of a sample from each plot are given in Table XXXVII. There is nothing in the figures obtained which indicates that dusting with sulphur resulted in an increased yield of grain or 1000 grain weight by controlling the disease. As indicated in a previous paragraph, the disease was largely controlled in mid July by the warm weather and very little infection developed on the ears.

From the simple experiment just described and also from figures for yields obtained from farmers whose crops were fairly severely infected on the leaves early in the season, it does seem that unless the heads of a crop are attacked by yellow rust little reduction in yield occurs. Farmers whose wheat crops were quite severely infected with yellow rust early in the season were quite satisfied with the final yields in 1949. However, there is the argument of what the yields might have been if there had been no rust present at all.

The writer is hoping to carry out some work on these points at Cambridge. For example, is leaf infection really important? If it is then at what stage? And so on.

PART VI

THE RELATIONSHIP OF METEOROLOGICAL CONDITIONS
TO THE INCIDENCE OF YELLOW RUST IN EACH SEASON

1. INTRODUCTION

The effect of climate on yellow rust has not received anything like the attention that it has on black rust. The two problems are in many ways completely different and therefore have to be treated in a different manner. Black rust virtually starts afresh each spring. In TABLE XXXVII fungus is

THE TOTAL GRAIN AND 1000 GRAIN WEIGHT OF EACH SAMPLE

one needs to consider the relationship between climate and the fungus from April only. It has been shown that as far as direct infection of cereals and

Plot No.	<u>Dusted</u>			<u>Undusted</u>		
	1	3	5	2	4	6
Total grain (grms)	293	335	376	349	321	307
1000 grain weight (grms)	44.36	44.05	44.06	42.26	44.54	44.17

It is then a comparatively straightforward matter to examine the meteorological records and to connect the development of the disease with the prevailing weather conditions.

Yellow rust on the other hand presents a far more complicated problem. With the facilities available it is impossible to know anything about the amount of inoculum present and its origin. When attempting to account for an attack of yellow rust in any part of the season, questions which immediately spring to mind are - has there been a fresh influx of spores from where the rust has previously become established? Have the local climatic conditions been

PART VI

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1. INTRODUCTION

The effect of climate on yellow rust has not received anything like the attention that it has on black rust. The two problems are in many ways completely different and therefore have to be treated in a different manner. Black rust virtually starts afresh each spring. In Scotland the fungus is inactive between about December and mid March, and one needs to consider the relationship between climate and the fungus from April only. It has been shown that as far as direct infection of cereals and grasses is concerned nothing is carried over the winter. One can note the time of germination of teleutospores, observe the first appearance of spermatia and subsequent aecidiospores and uredospores. It is then a comparatively straightforward matter to examine the meteorological records and to connect the development of the disease with the prevailing weather conditions.

Yellow rust on the other hand presents a far more complicated problem. With the facilities available it is impossible to know anything about the amount of inoculum present and its origin. When attempting to account for an attack of yellow rust in any part of the season, questions which immediately spring to mind are - has there been a fresh influx of spores from where the rust has previously become established? Have the local climatic conditions been

favourable so that generations of spores have been produced in quick succession, thus giving a large supply of inoculum near at hand?

Observations in Scotland have rather indicated that yellow rust is virtually always present. After a mild winter, uredospores of the rust can easily be found in March and can usually be found in December each year. Doubtless then, with careful searching viable uredospores could be found in January and February. These two months occupy about nine weeks and during the cool conditions which usually then exist, the incubation period of the rust could easily be prolonged to this length of time. Mehta (1923) found that even in comparatively mild winters the incubation period in some of his experiments with yellow rust was prolonged to five or six weeks. He suggests that this long incubation period provides an explanation of the phenomenon of spontaneous outbreaks of the disease over large areas within the space of a few days. Straib (1938) commenting on new infections during the winter months states that they are particularly favoured by the higher infective capacity of winter uredospores, which also remain viable for a longer period than summer spores.

Thus it is highly probable that in S. E. Scotland yellow rust is always present, except perhaps in severe winters. The amount of potential inoculum available, however, is never known.

When considering black rust, certain seasons could be grouped as being seasons of severe rust, and others as seasons of slight rust. On the other

hand, the progress and intensity of yellow rust is different each season and therefore grouping of seasons is not usually possible. Thus, in attempting to link up the development and spread of yellow rust with the prevailing meteorological conditions, except for a few generalisations, most years will require separate treatment.

2. A REVIEW OF SOME OF THE LITERATURE ON THE TEMPERATURE, HUMIDITY, AND LIGHT RELATIONSHIPS OF YELLOW RUST.

(i) The temperature relationships of yellow rust.

The uredospores of yellow rust are known to withstand cold much better than do those of black rust. Mehta (1923) found that at the relatively low temperature of 37° F he obtained better germination (20 to 30%) with yellow rust spores than with spores of either black or brown rust. Between 41° and 68° F Mehta obtained good germination with the three rusts. Stroede (1933) agrees with Mehta's findings. Ling (1945) states that yellow rust uredospores germinate best at 52° F, the minimum and maximum for germination being just above freezing point and 77° F respectively. A temperature below 50° F was found by Straib (1940) to be the optimum for germination 34° being the minimum and 77° F being the maximum. Newton and Johnson (1936) obtained the best germination at 50° to 54° F, and observed a sharp decline in germination at temperatures below 41° and above 68° F.

For infection and subsequent development of the organism within the host the optimum temperature

according to Naoumova (1937) lies between 59° and 77° F. She found the shortest incubation period (eight days) occurred when the diurnal temperatures were 59° to 77° F and the longest (21 days) with diurnal temperatures of 37° to 41° F. She also found the critical temperatures for appearance of pustules were a night minimum of about 37° and a day maximum of about 77° F. Newton and Johnson (1936) observe that as with black rust the optimum temperatures for rust development are slightly higher than those for spore germination. Straib (1940) also confirms this.

Numerous workers have drawn attention to the fact that as the temperature rises above the optimum, varieties which are susceptible to the rust at the optimum temperature become increasingly resistant. For example, Newton and Johnson (1936) have shown that a temperature of 77° F for a period of ten to twelve hours each day rendered a susceptible host resistant to the rust, even when the temperature during the rest of the day was congenial to rust development. It has also been shown that the various physiologic races behave differently in their response to high temperatures.

Most workers agree that severe outbreaks of yellow rust are associated with cool weather. Beauverie (1923) commenting on the winter preceding an epidemic season states that it was very mild. Then in the first eight days of May temperatures were high resulting in vigorous vegetative growth,

rendering the plants susceptible to the disease. The temperatures then dropped and it remained cool until July. Under such conditions the rust continued producing uredospores all the summer, leading up to epidemic proportions. Ling (1945) picks out the month of April as being one of importance. In an epidemic year the average mean temperature of the month was about 50° F lower than in seasons of little rust. In Italy (Potenza 1928) it was found that low temperatures are necessary for infection. Newton and Johnson (1936) commenting on the limited spread of the rust towards eastern Canada state that it is the high day temperatures which prevail in the prairie provinces during the summer months which prevent the growth of the rust during that period. It is only during autumn when the day temperatures get lower that the rust becomes prevalent.

(ii) The humidity relationships of yellow rust

The importance of moisture for rust spore germination and subsequent development within the host has been stressed previously when dealing with black rust. No further discussion on this point need therefore be given.

(a) Amount of rainfall

In Germany Becker and Hart (1939) came to the conclusion that for the development of the rust, heavy annual rainfall was necessary. The disease can only thrive when there is a plentiful water supply to the plant, conducive to vigorous growth. Ling (1945) reporting on yellow rust in

China considers the extent and distribution of the late winter and spring rainfall to be of outstanding importance. In 1939 an epidemic year, the winter and spring rainfall was about half an inch and four inches greater respectively than in years of little rust. A study of meteorological data in Argentina (Humphrey & Cromwell 1930) showed that in an epidemic year the rainfall in the spring as well as in the previous autumn was above average, and that the summer rainfall was three inches above average. Beauverie (1923) reports that the rainfall in October and April preceding a summer of epidemic rust was four inches and one inch respectively above average. Beauverie's work led him to believe that there was a 'critical period' of thirty days before the appearance of the ears and ten days afterwards when the weather exercises the maximum effect upon the crop. In a year of severe rust the rainfall during this 'critical period' was about half of the average.

There are, however, some conflicting reports in the literature on the rainfall during epidemic seasons. Moore (1948) writing about the epidemic in England in 1943 remarks on the dryness of February, March, and April. The May rainfall, on the other hand was found to be above average.

(b) Relative humidity

Potenza (1928) writes that infection is favoured by high humidity. Straib (1940) reports that for yellow rust, the period needed for the production of full infection in a saturated atmosphere is shorter than in any other of the cereal

rusts. In 1939 which was a year of severe rust attack Ling (1945) calculated that the average mean relative humidity for the months February to April was 81.3%, while for the same months in two years when yellow rust was scarce, the average mean relative humidities was 77.2 and 76%.

(iii) The light requirements of yellow rust

The statements made in the literature which deal with the light requirements of the rust are somewhat divergent. Stroede (1933) states that both natural and artificial light retard the germination of yellow rust spores. Sibilia (1928) on the other hand was unable to obtain germination of uredospores in darkness. The wheat form of Puccinia glumarum was found by Gassner and Straib (1928) to be much more susceptible to external conditions than other cereal rusts. Thus the incidence of infection of wheat by yellow rust was greatly reduced by the partial or total absence of light. Also, four hours exposure to direct sunlight at 86° to 95° F almost completely killed the spores of yellow rust, whereas those of the brown, black and crown rusts were unaffected. In a later paper (Straib 1940) experiments showed that uredospore germination as measured by germ tube growth proceeds more rapidly in subdued daylight than in absolute darkness, at least at temperatures below 59° F. Below this temperature, no difference in germ tube growth was perceptible. In this paper Straib also reports that infection can take place in absolute darkness.

3. METEOROLOGICAL CONDITIONS AND YELLOW RUST IN S. E. SCOTLAND

(i) The disease each season

The general development of the disease in each season from 1943 to 1949 has been described in a previous section. For convenience, a brief summary is given here, before proceeding to discuss the relationship of meteorological conditions to the disease.

1943: The rust appeared early in the season and apparently spread and increased in intensity up to harvest. Probably the worst year for rust.

1944: A certain amount of rust present. In no way severe.

1945: Very little rust.

1946: The rust was present early in April and increased until about mid May. It then decreased from the end of May to July, and then appeared to increase again in August.

1947: The rust did not appear until the end of June and then soon died out again.

1948: The rust appeared mid May and became rather widespread and fairly severe.

1949: The rust was found very early in the season, i.e. in March. It increased to become fairly severe until mid July when the attack rapidly died out.

(ii) The meteorological data

For yellow rust considerations the meteorological

data from three stations have been examined, the stations being North Berwick, Kelso and Eskdalemuir. These stations are all situated in the area south of the Forth and have been chosen because most of the writer's observations were made in this area. The North Berwick records are not always very helpful. An inland station would probably have given results more suitable to the present problem but North Berwick is the best station in its area.

(iii) Temperature relationships

Data from North Berwick, Kelso and Eskdalemuir on the average mean maximum and minimum temperatures for the months November to August for each season are presented in Tables XXXVIII, XXXIX and XL. The seasons are arranged roughly in order of severity of rust attack with 1943 being the worst season.

(a) The years of little or no rust (1945 and 1947)

The following is an account of the relationship between climate and yellow rust during the seven years 1943-9.

The tables give an indication immediately why yellow rust was so very little in evidence during 1945 and 1947. The winters (here being taken as the months November to March) preceding these two seasons were the coldest of all the winters here considered. November 1944 to January 1945 was a very cold spell and the first three months of 1947 provided some unusually low temperatures. The winter cold would then have been very unfavourable for rust survival. Then also the late spring and summer temperatures were above average, and higher than in any of the

TABLE XXXVIII

THE AVERAGE MEAN MAXIMUM AND MINIMUM TEMPERATURES ($^{\circ}\text{F}$) FOR THE MONTHS NOVEMBER TO AUGUST
AT NORTH BERWICK

	1942-3		1947-8		1948-9		1943-4		1945-6		1944-5		1946-7		Average	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Nov.	46.6	35.2	49.7	38.1	51.9	38.9	47.9	38.6	50.2	41.0	46.1	35.4	50.4	40.2	47.4	37.2
Dec	48.0	37.4	45.7	36.2	47.5	36.8	44.1	34.9	46.1	36.4	43.9	34.8	43.0	32.8	44.2	35.7
Jan	42.9	34.7	42.6	34.0	48.1	35.1	46.9	35.9	43.1	31.3	38.0	28.3	-	33.0	44.5	34.8
Feb	48.3	37.2	50.1	34.9	47.9	35.7	44.0	34.3	46.3	35.8	48.3	37.5	-	26.9	44.1	34.7
Mar	49.9	37.5	52.5	37.3	48.3	34.4	48.1	35.1	47.6	35.7	53.4	39.4	-	28.4	47.6	35.7
Apr.	56.6	42.6	54.5	37.9	55.1	41.3	53.9	41.2	57.0	40.3	54.4	40.0	52.1	38.2	51.2	38.1
May	57.5	42.2	56.7	40.2	60.8	42.1	55.7	43.4	55.9	41.6	57.1	42.0	54.5	42.6	55.8	42.1
June	62.8	47.9	61.5	46.6	63.5	47.1	60.3	46.4	61.8	46.3	62.3	47.5	62.0	48.6	62.2	47.0
July	64.9	49.9	65.4	49.9	68.5	51.8	63.9	51.8	66.5	51.9	67.1	51.8	64.5	51.3	66.8	51.7
Aug	62.9	50.9	62.4	49.7	67.3	52.3	64.5	51.5	63.1	49.4	64.5	50.7	66.5	52.1	65.5	50.3

TABLE XXXIX

THE AVERAGE MEAN MAXIMUM AND MINIMUM TEMPERATURES ($^{\circ}\text{F}$) FOR THE MONTHS NOVEMBER TO AUGUST
AT KELSEO

	1942-3		1947-8		1948-9		1943-4		1945-6		1944-5		1946-7		Average	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Nov.	46.0	32.4	48.1	33.9	50.1	35.6	46.2	34.9	48.0	40.0	44.6	33.8	48.6	37.7	46.9	34.7
Dec.	48.5	36.1	42.7	32.8	45.4	33.3	41.9	32.2	43.9	34.4	42.6	33.7	41.1	29.9	43.6	33.2
Jan.	42.8	31.4	40.6	32.0	46.0	32.5	46.3	35.1	40.6	30.7	36.4	24.9	39.4	30.0	43.1	32.5
Feb.	50.0	35.7	44.2	33.4	47.4	33.4	43.1	33.1	46.0	35.7	48.9	36.8	34.4	22.7	44.2	32.3
Mar.	50.4	35.9	52.8	34.5	47.3	31.5	47.9	34.0	47.6	34.3	52.5	38.5	39.4	25.4	47.6	33.4
Apr.	55.0	41.3	53.5	36.7	56.3	39.3	55.0	40.6	58.0	41.5	56.0	38.9	50.0	37.2	52.3	36.1
May.	58.6	41.0	58.7	39.6	59.9	40.4	57.2	42.0	58.6	42.2	58.0	44.2	59.7	42.6	58.6	41.5
June	62.5	47.8	60.8	45.9	65.8	45.1	62.7	45.8	61.7	47.0	63.8	46.2	62.4	49.1	64.0	45.9
July	64.3	48.7	65.9	50.2	68.5	51.4	66.2	51.5	65.5	-	68.4	51.6	66.4	51.0	66.6	49.9
Aug.	61.8	48.5	62.9	45.9	67.7	50.2	67.6	50.7	62.5	46.0	65.8	48.0	71.9	51.0	65.7	49.3

TABLE XL

THE AVERAGE MEAN MAXIMUM AND MINIMUM TEMPERATURES ($^{\circ}\text{F}$) FOR THE MONTHS NOVEMBER TO AUGUST
AT ESKDALEMUIR

	1942-3		1947-8		1948-9		1943-4		1945-6		1944-5		1946-7		Average	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Nov.	45.4	30.9	45.7	33.6	47.4	35.3	45.1	34.2	47.8	37.4	43.5	33.2	46.9	37.9	44.2	33.3
Dec.	45.1	35.0	42.6	33.7	43.2	32.3	40.9	32.0	43.2	31.6	40.6	32.3	39.6	29.1	41.4	32.4
Jan.	40.4	32.2	39.0	32.1	43.0	32.6	43.9	33.9	39.2	26.9	35.5	24.2	38.0	29.4	40.8	31.4
Feb.	45.7	35.4	42.3	31.5	44.0	32.6	41.4	29.5	44.2	31.6	45.1	35.1	31.3	22.6	41.3	30.9
Mar.	48.0	32.7	52.0	33.9	45.9	30.8	46.7	30.6	45.1	30.5	49.6	34.3	36.9	27.5	44.3	31.0
Apr.	52.5	38.6	52.2	34.7	51.8	38.4	52.4	39.0	53.6	35.0	53.1	35.1	47.9	34.5	49.0	33.3
May	57.2	37.1	59.0	36.5	57.5	37.0	55.3	38.0	58.6	36.7	56.7	39.1	59.2	41.0	55.8	38.8
June	60.8	44.1	59.4	44.9	64.8	43.9	60.1	43.8	59.1	40.8	60.4	45.0	60.8	47.7	60.7	43.3
July	64.0	46.4	63.9	48.2	65.5	47.7	63.9	49.6	62.0	48.3	65.5	48.1	63.8	49.6	63.3	47.6
Aug.	60.9	46.7	59.4	46.8	63.4	50.3	65.2	47.9	60.4	44.7	65.0	46.4	71.6	49.7	62.0	46.9

other seasons. Thus even if infection had been present, the late spring and summer temperatures would have been too high for the development of the rust. It will be remembered that 1945 and 1947 were years of severe black rust.

- (b) The years when at least a certain amount of rust was present.

During the months November to March for 1942-3, 1947-8 and 1948-9 the average mean temperatures were generally speaking the highest of all the years under review. The seasons following these three winters were those with the most yellow rust. The average mean temperatures for the same months for 1945-6 are similar and about equally high. Thus if the winters are mild, yellow rust will appear early in the following spring.

1943: The April of 1943 was about the warmest of the seven years under review and, following as it did a mild winter, conditions must have been very favourable for rust infection. For the time of year the incubation period was undoubtedly very short and generations of spores would have been produced in quick succession building up a considerable amount of inoculum. The mean temperatures for May were about average, while the June to August means were below average. In 1943, therefore, the worst year for rust, meteorological conditions must have been very favourable. The previous winter was very mild, and it was followed by above average temperatures in

spring with summer temperatures below average.

1944: No detailed observations on the rust have been obtainable for 1944. The rust was not present to any serious extent as otherwise records would be available. Except for a few generalisations the writer cannot therefore, give the 1944 season much attention. The meteorological records generally indicate that the rust should have been at least fairly prevalent. After the considerable quantity of inoculum which must have been present in the late autumn of 1943, and in view of the rather mild winter it is difficult to see how the rust could have failed to survive and have been present in quite appreciable amounts. It is interesting to note that Moore (1944) also found it difficult to explain the relative scarcity of rust in 1944.

1946: Following the mild winter the rust appeared early in 1946. The February to May temperatures were above average and the rust increased during these months. However, in the succeeding two months the rust failed to develop to any extent and even died out in certain places. There is little in the temperature data to account for this, but the humidity conditions considered later do provide an answer to some extent.

1948: Although the winter of 1947-8 was a fairly mild one the rust was not seen until May in 1948. This was probably due largely to the almost

complete absence of yellow rust in the autumn of 1947. The rust had, so to speak, considerable leeway to make up. The temperatures during April and the early part of May were rather low, probably retarding rust development. From mid May the temperatures rose and from then until August were similar to those obtaining in 1943, and the rust developed rather quickly and spread. It is probable that if the rust had developed earlier in the 1948 season it would have become severe by harvest.

1949: Although the months March and April were not as warm in 1949 as they were in 1943 the average temperatures for the period November to March were about equal in the two years and the rust became obvious very early in 1949. The May and June temperatures were very similar in 1949 to what they were in 1943 and the rust developed and spread fairly rapidly becoming severe on many crops. However, in July and August the temperatures rose considerably and coupled with the drought conditions prevailing at the time, the rust died out rapidly and fresh uredosori were difficult to find. From an economic point of view the high temperatures came just at the right time. If the weather had continued cool, the ears of rusted wheat crops would have been attacked and reduction in yields would doubtless have followed.

(c) Points of special interest in the
Eskdalemuir records.

It is interesting to note in the Eskdalemuir records that from November to May in the seasons 1943-4, 1945-6, 1944-5, and 1946-7 there is at least one month with a mean minimum temperature of below 30° F. This is not so in the other three seasons considered, i.e. the seasons in which the rust was most prevalent. It can be seen also that the lower the temperature below 30°, and the more months in which it occurred, the less was the quantity of rust present in the following season. In February 1944 the mean minimum was 29.5°, in January 1946 it was 26.9, in January 1945 it was 24.2 and from December 1946 until March 1947 the mean minima were all below 30° F.

This relationship will probably not always hold because spring and summer conditions are obviously of importance in determining the development of the rust, but at Eskdalemuir for the seven years under review, the feature is clearly marked.

The Eskdalemuir station keeps many records in great detail, among them being a record of the temperature taken each hour. The mean of twenty four hourly readings is a better figure for the daily mean temperature than the figure obtained from the maximum and minimum readings. Table XII contains the mean temperatures, obtained from hourly readings, for the months January to August in the years when rust was present (i.e. 1945 and 1947 have been omitted.)

As previously stated the rust appeared very early in 1943 and 1944 and the Table indicates that the January and February temperatures were highest in these two years.

The March to June average mean temperatures for the three years when rust developed to quite serious proportions (1943, 1948 and 1949) are appreciably higher than for the same months in rather less severe rust years. In 1946 the mean

TABLE XLI

THE AVERAGE MEAN TEMPERATURES ($^{\circ}$ F) COMPUTED FROM HOURLY RECORDS FOR THE MONTHS JANUARY TO AUGUST AT ESKDALEMUIR.

	1943	1948	1949	1944	1946
January and February	38.4	36.3	38.4	37.6	35.7
March to June	46.7	46.4	46.3	45.6	44.9
July and August	54.5	54.7	56.8	56.6	56.4

4. (iii) Humidity relationships

(a) Amount and number of days of rain

Tables XIII, XIII, XIV contain data on the amount of rainfall and number of rain days in the months November to August for the seven years 1943-5, to 1949.

It has already been shown that the very slight amount of yellow rust present in 1945 and 1947 was a result of the low temperatures experienced in the winters preceding these seasons. Temperature is then apparently more important than rainfall in its effect

As previously stated the rust appeared very early in 1943 and 1949 and the Table indicates that the January and February temperatures were highest in these two years.

The March to June average mean temperatures for the three years when rust developed to quite serious proportions (1943, 1948 and 1949) are appreciably higher than for the same months in rather less severe rust years. In 1946 the average mean temperature for these months was the lowest of the five years here considered. It will be remembered that the rust did die out to some extent during May and June 1946. The temperature figure suggests that conditions were unfavourable for rust development.

In 1943 and 1948, the years when rust increased throughout the latter part of the season, July and August were relatively cool months. The July and August average mean temperatures for each of these two years are about two degrees lower than in the same months in the other years.

4. (iv) Humidity relationships

(a) Amount and number of days of rain

Tables XIII, XIII, XIV contain data on the amount of rainfall and number of rain days in the months November to August for the seven years 1942-3, to 1949.

It has already been shown that the very slight amount of yellow rust present in 1945 and 1947 was a result of the low temperatures experienced in the winters preceding these seasons. Temperature is then apparently more important than rainfall in its effect

TABLE XLII

THE AMOUNT OF RAINFALL (INCHES) AND THE NUMBER OF DAYS OF .01 INCH OR MORE RAIN FOR EACH MONTH FROM NOVEMBER TO AUGUST AT NORTH BERWICK

	1942-3	1947-8	1948-9	1943-4	1945-6	1944-5	1946-7	Average
	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	
Nov.	0.43 6	2.13 18	1.92 12	0.71 14	0.75 12	4.44 20	4.03 20	2.24
Dec.	0.75 15	1.93 19	1.44 13	0.90 12	1.88 17	1.52 17	1.88 20	2.15
Jan.	1.67 19	5.47 25	1.53 9	1.12 10	1.43 12	4.40 24	1.97 19	1.72
Feb.	1.00 12	1.57 14	0.49 10	1.10 8	1.08 9	1.51 15	1.15 15	1.56
Mar.	1.41 8	0.45 9	1.21 14	0.33 6	2.43 18	0.79 9	4.20 18	1.88
Apr.	0.81 9	1.35 23	1.12 14	1.95 11	0.17 3	1.39 12	1.84 14	1.40
May	3.42 15	1.38 15	1.72 11	1.50 17	2.22 14	4.11 19	3.92 18	1.99
June	1.66 12	2.48 15	1.39 9	3.11 15	2.47 16	1.87 17	2.55 19	1.66
July	2.46 13	1.21 9	1.77 12	2.35 16	3.18 17	2.33 11	1.83 9	2.58
Aug.	3.32 19	7.68 18	2.20 13	2.99 11	2.98 15	2.78 11	0.16 4	3.16

TABLE XLIII

THE AMOUNT OF RAINFALL (INCHES) AND THE NUMBER OF DAYS OF .01 INCH OR MORE RAIN FOR EACH MONTH FROM NOVEMBER TO AUGUST AT KELSEY

	1942-3	1947-8	1948-9	1943-4	1945-6	1944-5	1946-7	Average
	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	
Nov.	0.36 8	2.87 16	1.82 12	1.45 17	0.81 13	4.94 25.	4.37 22	2.31
Dec.	1.15 19	1.84 17	1.88 15	0.81 11	1.66 16	1.96 18	1.60 20	2.32
Jan.	2.68 8	6.04 21	2.21 10	1.05 13	1.53 18	4.25 22	1.87 22	1.75
Feb.	1.13 13	1.64 18	0.64 11	1.47 19	0.83 12	1.88 18	2.20 19	1.70
Mar.	1.20 9	0.78 7	1.09 9	0.98 15	1.26 12	0.61 11	4.06 23	1.95
Apr.	1.13 14	2.23 11	1.35 14	1.51 10	0.49 11	1.12 15	3.94 19	1.57
May	3.97 20	1.33 12	1.35 13	2.73 12	1.59 13	4.30 21	2.91 19	1.93
June	3.55 21	4.39 22	0.87 8	2.56 20	1.56 17	1.97 18	4.28 22	2.11
July	3.16 12	1.13 13	2.39 7	2.39 16	2.61 18	1.97 16	2.87 19	2.63
Aug.	3.51 24	10 46 30	2.17 14	1.65 11	4.64 15	2.16 18	0.22 2	2.95

TABLE XLIV

THE AMOUNT OF RAINFALL (INCHES) AND THE NUMBER OF DAYS OF .01 INCH OR MORE RAIN FOR EACH MONTH FROM NOVEMBER TO AUGUST AT ESKDALEMUIR

	1942-3	1947-8	1948-9	1943-4	1945-6	1944-5	1946-7	Average
	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	Inches Days	
Nov.	1.39 13	8.98 20	5.51 18	4.30 18	0.70 18	9.92 25	10.71 27	5.80
Dec.	9.04 27	2.75 19	7.64 20	2.68 20	3.47 20	8.61 23	6.63 19	7.00
Jan.	8.18 26	10.52 25	7.01 20	7.73 25	7.56 20	6.24 24	6.52 24	5.40
Feb.	5.50 18	5.92 18	6.46 21	3.74 18	3.99 17	8.18 27	1.21 16	4.95
Mar.	2.37 15	3.85 14	2.52 15	0.67 11	5.26 18	4.57 16	5.70 23	4.90
Apr.	4.02 22	5.08 18	6.43 21	3.71 18	1.97 12	3.61 15	9.98 24	3.40
May	6.51 17	1.77 11	3.26 16	3.83 18	1.31 10	6.15 20	3.51 21	3.30
June	6.38 24	6.93 20	1.34 10	5.58 22	6.41 22	5.17 24	4.94 23	3.15
July	3.63 17	3.99 14	2.64 12	3.13 15	4.58 20	3.93 15	4.50 21	4.10
Aug.	7.81 27	9.84 20	3.67 14	4.21 14	6.25 26	2.00 12	0.03 1	5.15

upon the overwintering of the rust and these years need little further consideration. It will be seen from the tables that the rainfall in the winters preceding these seasons was above average, and was by far the greatest amount which fell during any of the winters here considered.

Generally speaking the rainfall in winters preceding seasons when yellow rust is present is well below average. The winter of 1947-8 is at first sight an exception, but it should be noticed that of the months November to March, January was the exception in experiencing heavy rainfall. Thus for overwintering of the rust low winter rainfall is apparently the requirement.

From the severity of attack the 1943 meteorological conditions were apparently ideal and it can be seen in the tables that the rainfall from May to August was generally rather above average in that year. In 1948 and 1949, the other rust years, although the rust was probably not as serious as in 1943, the rainfall from May to August was also about average.

Attention was drawn in a previous paragraph to the difficulty in showing why the rust did not develop to any serious extent in 1944. There is very little in the rainfall tables to account for it, but it will be seen that the November 1943 to March 1944 was at each station rather low; lower than in any of the bad rust years.

In 1946 the rust was found in the field early in the season but later (end of May to July) appeared to

decrease. Many new infections were noticed again in August. The temperature conditions it will be remembered gave no clue as to why this should have happened. It is therefore necessary to examine the rainfall data rather more closely in an attempt at finding a reason for this erratic progress of the rust.

Examination of Tables XIII, XIII and XIV will show that at the three stations the rainfall for each month from November 1945 to March 1946 was below average. The total winter rainfall preceding the 'ideal' 1943 season was also below average, but except at North Berwick, each month's rainfall was not consistently below average. This in itself is not sufficient to account for the decrease in amount of rust from the end of May until August 1946. Now consider the April and May rainfall in 1943, 1944, 1948 and 1949. The total rainfall for April and May together with the number of days on which it fell are given for each station in Table XLV. From this table it can be seen that the April and May 1946 rainfall was the lowest of the five years given. 1949 is the nearest in its quantity of rainfall, but even that is considerably greater than the 1946 rainfall. The number of days on which rain fell is also least in 1946. It should be remembered too that in 1946 the rain which fell in the previous November to March was considerably less than in most years.

The shortage of rain during April and May must then have been largely responsible for the dying out of the fungus during the end of May and June. The temperatures during this period were, generally speaking,

TABLE XLV

THE TOTAL APRIL AND MAY RAINFALL (INCHES) AND NUMBER OF RAIN DAYS FOR THE YEARS OF YELLOW RUST

	1943		1948		1949		1944		1946	
	Total rain	No. days	Total rain	No. days	Total rain	No. days	Total rain	No. days	Total rain	No. days
N. Berwick	4.23	24	2.73	38	2.84	25	3.45	28	2.39	17
Kelso	5.10	34	3.56	23	2.70	27	4.24	22	2.08	24
Eskdale-muir	10.53	39	6.85	29	9.69	37	7.54	36	3.28	22

TABLE LVI

ESKDALEMUIR DURATION OF RAINFALL IN HOURS FOR CERTAIN NAMED MONTHS

	1942-3	1947-8	1948-9	1943-4	1945-6	1944-5	1946-7
Nov. - March	464.9	589.7	535.1	419.5	456.0	739.1	727.7
April - May	157.1	125.8	171.1	193.5	87.3	214.2	220.8
June - August	288.8	298.6	172.8	247.5	356.2	223.2	232.7

TABLE XLVII

THE RELATIVE HUMIDITY AT TWO STATIONS FOR THE MONTHS FEBRUARY TO MAY, AND JUNE

		1943	1948	1949	1944	1946
Kelso						
	Feb. - May	93	88	85	83	78
	June	85	89	81	80	78
Eskdalemuir						
	Feb. - May	81	80	82	80	79
	June	84	83	78	80	82

favourable, but rainfall was the limiting factor. The end of June and July brought a considerable increase in rainfall and conditions became more favourable for the rust as witnessed by the increasing amounts of infection which appeared.

In 1948 the rainfall was apparently favourable, particularly after May when the fungus was first found in the field. The March rainfall was very much below average and together with the relatively low temperatures prevailing at the time probably contributed to the rust appearing rather late.

Except in February which was a very dry month, the rainfall preceding the 1949 season was apparently sufficient, though in no month was it high. The actual summer of 1949 was rather on the dry side, but as pointed out previously, the high temperatures of July and August were probably the chief cause of the rapid decrease in the development and spread of the fungus.

(b) Duration of rainfall

Table XLVI contains a summary of the records from Eskdalemuir on the duration of rainfall during certain months in the years under review. There is apparently little correlation between the duration of the rainfall in the winter months and the type of rust year which follows.

It can be seen, however, that in 1946 the number of hours during which rain fell in April and May was very much less than in any other year. This again indicating that rainfall was the limiting factor in that season.

(c) Relative humidity of the air

Details of the average relative humidity for the period February to May and the month of June are given in Table XLVII. The years 1945 and 1947 are not considered here because it has been previously shown why yellow rust was almost absent in these years.

From the Table it can be seen that in these months there is a distinct tendency for the relative humidity of the air to be higher in years of fairly severe (1948, 1949) and severe (1943) yellow rust than in years of rather slight rust (1944, 1946). In 1946 particularly, the relative humidity was considerably lower than in years when the rust was more severe.

(v) Light relationships

The only meteorological records which can be utilised in a consideration of the light requirements of yellow rust are the records of hours of sunshine.

The total number of hours sunshine for certain periods in each year are given in Table XLVIII for the two stations north Berwick and Eskdalemuir. No figures are available for Kelso. Examination of the figures given indicates that there is little or no relationship between the number of hours of sunshine in any of the periods of months given and the type of rust year.

TABLE XLVIII

THE SUNSHINE HOURS AT NORTH BERWICK AND ESKDALEMUIR FOR CERTAIN MONTHS

	1942-3	1947-8	1948-9	1943-4	1945-6	1944-5	1946-7	Averages
<u>N. Berwick</u>								
January - March	210.5	223.2	278.9	214.0	208.6	194.4	177.2	235
April - June	520.8	613.7	658.6	368.0	543.5	507.2	376.9	510
July - August	305.4	310.5	357.7	212.4	290.9	327.7	365.9	332
<u>Eskdalemuir</u>								
January - March	187.4	217.0	225.1	210.3	234.1	195.8	167.1	188
April - June	463.9	485.4	553.4	398.0	539.5	447.3	334.7	463
July - August	290.4	230.1	311.3	225.8	229.9	323.5	370.7	269

(vi) Conclusions

From the previous examination of the meteorological conditions and the incidence of yellow rust from 1943 to 1949, the following conditions appear to be necessary for a severe yellow rust attack during the summer months.

The previous winter should be mild with rainfall rather below average. The early spring temperatures should be higher than average (relatively speaking the higher the better) and be accompanied by about average rainfall. The summer months should be cool with a fair amount of rainfall, i.e. the rainfall above average. If these conditions are fulfilled it is highly probable that susceptible crops at harvest will be quite severely infected with yellow rust.

SECTION 3.

OTHER CEREAL RUSTS .

OTHER CEREAL RUSTS

The other cereal rusts which are found in S. E. Scotland are of no economic importance. These rusts are Puccinia triticina Erikss, P.hordei Otth, P.secalina Grove and P.coronata Corda.

The following summarizes the position of each rust.

1. PUCCINIA TRITICINA. Brown rust of wheat.

About six years ago a paper appeared which stated that this rust was unknown in Scotland (Dennis 1944). However, the writer has found the rust each season since 1946.

The rust usually appears at the end of July and can be found until about the end of October. In 1947 it was quite severe on many wheat crops and virtually took the place of yellow rust. In most seasons, however, the rust is slight or very slight in its attack.

Observations on wheat varieties in S. E. Scotland indicate that probably all commonly grown varieties are susceptible to the rust.

Teleutosori of the rust have not been found in the field. Roberts (1936) working in Cambridge also reports being unable to find naturally formed teleutospores.

2. PUCCINIA HORDEI. Dwarf brown rust of barley.

Wilson (1934) records this rust in the Tweed and Forth areas of Scotland. The writer has found the rust each season all over S. E. Scotland. It usually appears at the end of July. In 1947 and 1948

it was first seen on 30 July. The rust has never been found to be even moderately severe on a crop. A few sori only are present per plant. Uredo and teleutosori can be usually be found up to December.

It is well known that the rust forms an aecidium on Ornithogalum species. D'Oliveira (1939) was unable to find the aecidium in the field, but could produce it artificially. However, in 1948 the aecidium was found on O.pyrenaicum in Wiltshire (Dennis & Sandwith 1948). Ornithogalum is frequently found in S. E. Scotland, but the aecidia of P.hordei have not been seen on it, although looked for.

3. PUCCINIA SECALINA. Brown rust of rye.

Wilson (1934) records the rust in the Tweed, Forth, and Tay areas of Scotland. The uredospores appear each year during the middle of July and can be found on most of the rye crops in S. E. Scotland. In 1947 and 1948 the rust was quite severe in the Ladybank area of Fife.

Macdonald (1949) found the aecidial stage of the rust on Anchusa arvensis near St Andrews. Other records are rare. Wilson (loc. cit) states that there is a specimen of the aecidial stage in Johnston's Herbarium.

4. PUCCINIA CORONATA. Crown rust of oats.

Recent literature (Dennis & Foister 1942, Dennis 1944) has drawn attention to the fact that oat crops in Scotland are usually free from crown rust. This is probably due to the absence from Scotland of the alternate host Rhamnus catharticus. In his paper Dennis indicates that outbreaks of

crown rust in Scotland must originate from wind blown uredospores from a region where the alternate host is prevalent, such as Ireland or southern England.

The rust can usually be found from about the beginning of October on volunteer oat plants. It was quite widespread on such plants in 1947 but was rather rare in 1948.

In 1949 the rust was actually seen on 29 August on four standing crops in Fife. The rust was fairly widespread after this date.

programme. The two most important rusts are black or stem rust Puccinia graminis and yellow or stripe rust P. glumarum. The other rusts found on cereals, namely P. triticea, P. hordei, P. secalina and P. coronata are of no economic importance.

The Thesis is in three sections. The first and largest deals with black rust, the second section is concerned with yellow rust, and the very short third section contains some observations on the rest of the cereal rusts.

Section I opens with a few remarks on the general background of black rust work in Great Britain, and the reason for undertaking the study. The writer was fortunate to discover an interesting book written in 1809 about cereal diseases in S. Scotland which it was found has a direct bearing on the present study. Part II is concerned with this book.

The common barberry, the alternate host of the black rust fungus, has been found in many hedges in S. E. Scotland particularly in the Border counties.

SUMMARY

In July 1945 the writer joined the staff of the Edinburgh and East of Scotland College of Agriculture. He was concerned with advisory work in plant pathology in S. E. Scotland from that date until December, 1949 when he left for another post at Cambridge.

As its title implies, the Thesis is the result of a study of the cereal rusts in S. E. Scotland which constituted the writer's main research programme. The two most important rusts are black or stem rust Puccinia graminis and yellow or stripe rust P. glumarum. The other rusts found on cereals, namely P. triticea, P. hordei, P. secalina and P. coronata are of no economic importance.

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The common barberry, the alternate host of the black rust fungus, has been found in many hedges in S. E. Scotland particularly in the Border counties.

Part III deals with the occurrence of the barberry as observed in the past and also at the present time.

Mahonia aquifolium has also been found bearing aecidia of black rust and the form of the infection on the barberry as well as on this host is described.

The host range of the fungus is given in Part IV. As well as wheat, barley, oats and rye, fourteen genera of the grasses have been found bearing infection. The hosts together with notes on the time and form of infection are given.

Because of the large number of barberries, black rust can be found each season. However, the development and spread of the fungus has been found to differ markedly each season. Part V gives details of the seasonal development of the disease. The method of overwintering of the rust is also dealt with here.

Some work on the physiology of the rust is given in Part VI. Germination and method of inoculating with the various spore forms is given.

Aecidia on a few barberry bushes were found to be parasitized by another fungus. Part VII contains a few notes on this.

Part VIII is concerned with the results of inoculations aimed at identifying the physiologic form carried by many of the grasses.

A statistical study of the uredospores and teleutospores of the five commonly occurring physiologic forms is given in Part IX.

As indicated in the text P.graminis avenae is the important physiologic form in S. E. Scotland and the

physiologic races of this form present in the area have been determined, as described in Part X.

In 1945 and 1947 the rust was very severe on many oat crops in the Border counties. It was, therefore, thought worth while to attempt to ascertain the effect of the rust on the yield and quality of oats, at the same time looking for differences in susceptibility of some of the varieties commonly grown. To this end, plots of twelve varieties of oats were sown in 1948 and 1949 near barberries. These experiments and results are described in Part XI.

Observations were made from 1945 to 1949 on the incidence of black rust in S. E. Scotland. It was observed that the amount of infection varied considerably from one season to another. It has been shown in other countries that meteorological conditions are largely responsible for the rate of development and spread of the rust. Part XII is an account of the relationship between meteorological conditions and the development of rust in the seasons under review.

Part XIII is a short report of an examination of the meteorological conditions obtaining in the winters preceding each season in relation to the incidence of rust.

In 1947, 1948 and 1949, very detailed observations were made on the time of appearance of spore forms and general spread of the rust and Part XIV links up the development of the rust with the prevailing weather conditions.

Section 2, the account of yellow rust in S. E. Scotland opens with a short introduction on previous references to the rust in Great Britain, followed by notes on the host range. Part III is concerned with the development of the rust each season, from 1943 to 1949.

Each year the writer made notes in the field of the susceptibility of the different varieties in cultivation to yellow rust, a description of which is given in Part IV.

It was thought worth while investigating the effect of yellow rust on yield. Part V is an account of this work.

As with black rust, it was found that the development and spread of yellow rust varied each season. Part VI deals with the relationship between meteorological conditions and the incidence of the rust.

Finally, Section 3 summarizes the position of the other cereal rusts in S. E. Scotland.

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Addendum.

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APPENDIX 1

THE YIELD OF GRAIN AND PERCENTAGE OF SECONDS
HARVESTED IN THE 1948 EXPERIMENT

		<u>Total grain ozs</u>	<u>% 2nds</u>
<u>Row A</u>	Victory	62	19
	Eagle	175	29
	Star	150	18
	Star	153	17
	Sun II	155	26
	Supreme	180	17
	Marvellous	142	17
	Potato	128	21
	Ayr Commando	189	23
	Marvellous	220	15
	Eagle	224	21
	Yielder	174	9
<u>Row B</u>	Sun II	84	29
	S.84	139	14
	Onward	152	19
	Onward	138	18
	Victory	143	18
	Primus	21	high
	S.84	132	21
	Eagle	145	17
	Primus	38	27
	Supreme	195	15
	Ayr Commando	219	24
	Onward	230	10

		<u>Total grain ozs</u>	<u>% 2nds</u>
<u>Row C</u>	Victory	109	19
	Sun II	145	19
	Potato	113	29
	Potato	121	29
	Star	114	26
	Yielder	92	16
	Marvellous	162	18
	Supreme	177	16
	Yielder	200	16
	Ayr Commando	202	16
	S.84	225	17
	Primus	87	18

APPENDIX 2

OBSERVATIONS ON THE SUSCEPTIBILITY OF WHEAT
AND BARLEY VARIETIES IN THE FIELD

Observations on wheat varieties

1946 Observations made 25 July.

Winter wheat sown 31.x.45

Infection about 1%	- Als	Defiant
	Guardsman	Holdfast
	Jubilegem	Pilot
	Redman	Squarehead II
	Victor	Vilmorin 27
	Wilhelmina	Wilma
	Yeoman	

No infection seen	- Atle	Bersee
	Juliana	Squareheads
	Steadfast	Master

Spring wheat sown 29.iii.46

Infection about 1%	- Brons	Diamond II
	Kolben II	Red Marvel

1947 Observations made 4 August

Winter wheat sown 11.xi.46

Infection about 1%	- Als	Castle
	Eroica	Victor
	Virtus	Wilma
	Yeoman	

No infection seen	- Bersee	Defiant
	Eclipse	Ergo
	Holdfast	Hybrid 46

No infection seen	- Jubilegem	Juliana
	Little Joss	Pilot
	Rampton Rivet	Squarehead Master
	Squarehead II	Steadfast
	Vilmorin 27	Warden

Spring wheat sown 12.iv.47

Infection about 10%	- Regent	Renown
------------------------	----------	--------

Infection about 1%	- A1	A2	A3
	Hope	Karn	
	Progress	Pusa 4	
	Thatcher	W. Canadian Hard.	

No infection seen	- Apex	Atle
	Brons	Diamond II
	Fylgia	Kolben II
	Meteor	Red Marvel

1949 Observations made 2 August

Winter wheat sown 20.xi.48

Infection over 40%	- Als	Jubilegem
	Pilot	Yeoman

Infection 5 - 10%	- Castle	Eroica
	Holdfast	King II
	Recovery	Scandia III
	Squarehead Master	Victor

Infection 0.5 - 1%	- Juliana	Little Joss
	Rampton Rivet	Redman
	Scandia II	Steadfast
	Warden	

No infection seen	- Bersee	Marshall
	N.59	Squarehead II
	Staring	Vilmorin 27
Spring wheat sown 29.iii.49		
Infection about	- Brons	Kolben II
0.5%	Progress	
No infection seen	- Atle	Diamond II
	Fylgia	Karn
	Pondus	4138

Five varieties of Canadian spring wheat were grown in plots at Boghall for the first time in 1949. On 22 July, the varieties Redman, Regent and Saunders were severely attacked (about 80% infection). The leaves were dead and hanging useless on the stems. The variety Thatcher was not nearly as badly infected - about 20% only. No infection was seen on Cascade which is therefore apparently resistant to the races of yellow rust found in S. E. Scotland. The leaves of this variety were still quite green and functional at this time.

Observations on barley varieties

1947 Observations made 4 August

Winter barley sown 1.xi.46

Infection about 40%	- Belgian six row	Plumage Archer
	Pioneer	Weibull's Winter A
	Prefect	

Spring barley sown 12.iv.47

Infection about 1%	- Balder	Common
	Freja	Weibull's 4744
No infection seen	- Binder	Canton
	Danish Archer	Earl
	Freja	Golden Archer
	H.H.Cult 9	Kenia
	Plumage Archer	Rigel
		Ymer
	Triumph	

1949 Observations made 2 August

Spring barley sown 26.iii.49

Infection about 80%	- Montcalm	O.A.C.3
	Titan	
Infection about 40%	- Sanalta	
Infection 15-20%	- Vantage	
Infection 1-5%	- Carlsberg	Common
	Herta	Research
	Weibull's 4744	
No infection seen	- Bere	Craigs Triumph
	Lenta	Newcross
	Nordgaarden	Plush

As with the wheat varieties, it is interesting to note how very susceptible are most of the Canadian varieties (Montcalm; O.A.C.3, Titan, Sanalta and Vantage) to the strains of yellow rust present in S. E. Scotland.

On 1 August 1949, the wheat and barley plots growing on the Department of Agriculture's farm East Craigs, Edinburgh, were examined for the presence of yellow rust. The results are as follows:-

Winter wheat sown 25.xi.48

Infection about 40%	- Pilot	Victor
	Wilhelmina	
Infection 10-15.	- Gluten	Jubilegem
Infection 0.5 - 1%	- Als	Holdfast
	Rampton Rivet	Redman
	Wilma	Yeoman
No infection seen	- Bersee	Juliana
	Little Joss	Scottish Iron
	Squarehead Master	Vilmorin 27
	Squarehead II	
	Warden	

Spring sown wheat

Infection about 0.5 - 1%	- Diamond II	Karn
	April Bearded Atle	
	Brons	Fylgia
	Meteor	

Winter barley sown 25.xi.48

Infection about 40%	- Pioneer	Prefect
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Spring sown barley

Infection about 40%	- Balder	Binder
	Common	Craigs Triumph
	Freja	Kenia
	Maja	Rigel
	Ymer	

Infection about 10% - Canton Golden Archer

Infection about 5% - Plumage
 Archer

No infection seen - Spratt Archer

Note: Little or no infection present on the ears.